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THE COLORATION OF ANTHER AND CORBICULAR POLLEN

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Recently interest has been centered in bee literature upon pollen, its use by the honey-bee, appropriate substitutes for pollen during a dearth of that food item of the honey-bee, and the importance of the honey-bee in cross-pollination in agriculture.

Literature on pollen is quite diffuse. In the United States excellent work in pollen research has been made by such men as Young (1908) and Wodehouse (1935). Some pollen studies concern the morphology or external structure of the pollen grains, some are directed to their anatomy or internal structure, others consider the chemical constituents of pollen, pollen as a cause of hay-fever, etc.

Most of the pollen studies give little or no notice to the coloration of the pollen grains themselves, and yet it would seem to be one of the important points overlooked. Todd (1941) states that, "The color of pollen is of great economic importance to a beekeeper. Some of the coloring materials are fat-soluble in beeswax. They are the source of the yellow color in beeswax. Some pollens also contain water soluble coloring materials, and they appear to be responsible for the amber color of honey. The fresh nectars so far examined, even from plants that produce dark honey, appear to be colorless." Fischer (1890) one of the great recent investigators of pollen was one of the first to note the importance of pollen color to the student of pollen morphology. Related species of pollen are quite often similar and sometimes the species of a genus can hardly be distinguished from each other except by their color. Erdtman (1933) specifies that for a complete analysis of pollen forms in research, notes on their color are also desirable.

Early writers on pollen, such as Grew, Malpighi and others remarked about the coloration of pollen grains and gave some specific identifications. In the 19th century Francis Bauer gave some sketches of pollen with a word or two added about the color. More recently Armbruster and Jacobs (1929) and Oenike (1934–5) give notice to the color of pollen grains but presumably as seen under magnification. Wodehouse (1935) in his monumental work on pollen grains, dismisses the entire subject of coloration with a few introductory words on "the yellow powder" and there is no further reference to pollen colors in his extensive descriptions and classifications. Microscopical journals, the beekeeping journals and a few other writings make an occasional reference to the color of individual species of pollen, but no comprehensive study has been made of this subject.

CORBICULAR POLLEN

It should be noted at once that all color appraisals or emphasis on the importance of pollen color so far (except that of Todd) are for anther pollen, i. e., either the color of the pollen masses on the anthers of flowers or of the individual pollen grains examined. The color of pollen, however, after it has been gathered by the

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honey-bee and as it is seen by the beekeeper or other observer in the form of pellets being brought into the hive is somewhat different. This type of pollen the author will refer to hereafter as *corbicular* pollen, and this paper refers to the masses of anther pollen and of corbicular pollen and not to individual pollen grains. The word "corbicular" is not to be found in Webster's New International Dictionary (1942) but was used some years ago by Casteel (1912) in describing the process of pollen collecting by the honey-bee. Most naturalists and poets limit the color range of corbicular pollen, referring to it simply as "the golden dust" of the flowers, or the "golden grist" which the bees bring home, or it is spoken of as "the golden foam of pollen." Bee literature itself abounds in generalizations. The color of pollen is said to range from "cream to dark purple" or it may be "all shades, from black to white and many hues of the rainbow." Less frequently are "yellow, orange, red, brown or green" specified. Cheshire (1888) says that the returning bees bring back to the hive "colored material . . . some shade of yellow or orange . . . crimson, green and even black . . . " His further references are to the color of the anther pollen of the Rosebay Willow herb and of the Purple Loosestrife not to corbicular pollen. Sempers (1911) lists for the locality of Aikin, Md., 39 plants and 13 colors. Some of these colors seem to be for anther pollen, as "white for Boneset," "greenish white" for the Pear, while "brown" for Wintercress and White Clover seems to refer to corbicular pollen. Later (1912) he specifies corbicular pollen when he states that the honey-bee gathering pollen on the Wild Carrot formed "greenish-white pellets" to take home. Bisson and Vansell (1940) investigating the properties of beeswax list twenty-one plants and fifteen natural colors of the pollen. The reference seems to be to the anther pollen. Vansell (1942) describing pollination factors lists twenty-two plants and gives fifteen colors for the corbicular pollen and adds other load characteristics. Todd and Bretherick (1942) describing the composition of pollen, list thirty plant pollens. Of these six are anther pollens ("hand collected") arranged in five color categories and twenty-four are corbicular pollens ("from the bees") arranged in fourteen color categories. An annual feature of the British "Bee Keeping Annual" (1944) is the listing of forty-three English pollen plants and their arrangement in eleven color classes.

In none of the above writings however was any notice given to the factor of change of coloration. There is a definite need to distinguish between anther pollen color and corbicular pollen color. This paper intends to show that there is an appreciable difference in color between anther and corbicular colors of pollen.

COLOR

Color may have a variety of meanings. While color and hue are used more or less synonymously, in this paper it will be evident that color refers to the general classes of sensations evoked in the nervous system of the eye and hue is a more specific identification of the same. Coloration simply describes the pollen's state of being colored.

There are two classes of colors; the chromatic colors, as reds, yellows, greens and blues, and the achromatic colors, as white and black and the intermediate greys. The latter have no hue and differ from each other only to the extent of their difference or resemblance to white or black. The achromatic colors may be arranged in a scale from black to white with all the intermediate greys between. Median grey at the center would differ equally from black and white and other greys according to their sense differences. This series can be made into a scale by assigning ordinal numerals to each ascending grey from black as zero (0) through median grey, equal to four (4), on to white as eight (8). The same scale may be expressed in terms of percentages. The relationship expressed on this scale is called brilliancy. Thus, black or zero brilliancy; 1 or 12.5%, very low brill.; 2 or 25%, low brill.; 4 or 50% brilliancy; 6 or 75% brill.; 7 or 87.5% brill.; and so on

with 8 or 100% brilliancy. The extremes or ideal limits are not realized in practice. The Munsell system uses nine degrees of brilliance, called "value."

Hue is the attribute in respect to which we describe colors as red, yellow, green or blue or any intermediate between two of these. Arranged in a circle they form a color circle. All hues may be described in terms of the four psychologically primary hues red, yellow, green and blue. Red-yellow equally resembles and differs from red and yellow. Between each consecutive pair of primary hues many intermediates may be recognized. Thus arbitrary points of division can be established on the hue cycle, whence we have, red, yellowish-red, reddish red-yellow, red-yellow (midway between red and yellow), yellowish red-yellow, reddish-yellow, yellow, greenish yellow, etc. These steps represent equal visual and not physical intervals. The Munsell system uses ten principal hues and has one hundred hue steps in its color cycle.

Colors of the same hue and brilliancy may differ from each other in vividness of hue, that is in degree of difference from grey. This attribute is called saturation. In terms of these three attributes colors can be arranged in a tridimensional space or color solid, as Fig. 1. Two equal cones are placed base to base. The achromatic

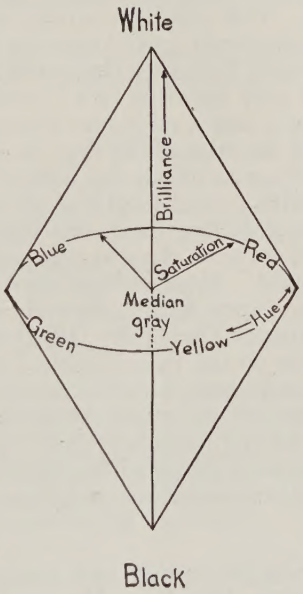

FIG. 1. Color Solid or Tridimensional Color Space. Hues are represented cyclically according to the hue cycle, on a plane perpendicular to the axis. The plane's level determines the brilliancy of the various hues. When close to the white apex colors are of great brilliancy and when close to the black point then they are of low brilliancy. Saturation is measured radially on each plane. Maximum saturation is at the rim and zero saturation is at the center.

white and black are represented by either apex, and the grey series of hues are along the vertical axis with median grey in the center. The vertical axis represents brilliancy. Corresponding to each degree of brilliancy is a plane perpendicular to the vertical axis and in this plane lie all the colors of equal brilliance. Hue is represented in each plane cyclically in the order of the color circle. Saturation is represented radially, with the axial points (greys) as reference points of zero saturation. The closer a hue is to the vertical axis, the less its saturation. Hues on the outer edge of the circle have the highest saturation. A scale of saturation similar to that of brilliancy above may be used.

To express hue, brilliancy and saturation, numerals may be used and they are referred to as color constants or dimensions. This author has used the ordinals (or the percentage values) only to represent saturation and brilliancy. To represent hue the author has used the colorimetric values of the various hues as expressed in wave lengths in millimicrons (mμ). These wave lengths and the scale values of saturation and brilliancy may be called the physical correlates.

COLOR VALUES

The values of the psychologically primary hues, referred to hereafter in the tables are the mathematical mean of the color range as given in The Handbook of Colorimetry (1936), i. e., red, 655 millimicrons (mμ); yellow, 580 mμ; green, 535 mμ; and blue 475 mμ. The values of the intermediates are taken from Judd's (1940) listing, as, yellow-red, 598 mμ; green-yellow, 566 mμ; and blue-green, 495 mμ. For yellowish-red, (English vermillion) 644 mμ; for reddish red-yellow, (Mineral Orange) 614 mμ; and for reddish-yellow (light Chrome yellow) 585 mμ, Rood's (1942) values were taken. The 591 mμ for yellowish yellow-red (Medium gold) is from Nutting (1931), and the Handbook of Colorimetry (1936) supplied the values of yellowish-green (Olive green) 572 mμ; and of yellowish yellow-green (Apple green) 568 mμ. The values of the greenish yellow-green hue, 550 mμ, and of yellowish green 540 mμ are interpolations of this author.

COLOR MATCHING

This entire study it should be noted is not one of color analysis but of color-matching. No spectroradiometer or spectrophotometer was used. The method of color-matching used by the author is the one suggested in A Dictionary of Color (1930). This volume contains reproductions of about 7,000 different colors, but plates numbered 1 to 24 showing the spectral colors from Red to Orange, Orange to Yellow and Yellow to Green (about 2,000 in all) were the most useful. A sheet of neutral grey paper having a reflection factor of about 42.9% was used as a mask to bring a single color into immediate focus. An opening of 9 square millimeters reduced the area of the hue "samples" to a minimum. The color mask was used at all times to check the individual anther or corbicular pollen masses. A linen tester with a focal length of 50 millimeters giving about four magnifications (4×) aided in checking the pollen masses. The illumination used was that of natural daylight on such days as might be termed clear and sunny. Direct sunlight was never used. Most pollens were rechecked within doors under a window having northern exposure, but showed no difference. The color charts of Webster's New International Dictionary (1942) were used to a limited extent and those colors are identified on the list of Table I by the lower case letter "w." Not every hue or color has a name, hence some are referred to only by Plate number, by the column letter and by the row number, as, 9 E 2. At times a closely related color is suggested for the unnamed hues. This is indicated by the symbol $\approx$. The author believes he is gifted with normal color vision and the maximum time required for each pollen color check was about twenty minutes.

FIELD METHODS

During the spring and summer seasons of 1944 and 1945 visits were made afield in the New York Metropolitan district and to the Brooklyn and New York Botanical Gardens for anther and corbicular pollen specimens. The characteristic movements, as described by Casteel (1912) and the tell-tale results in the corbiculae of the honey-bee served to distinguish and identify the pollen gatherers from the nectar gathering honey-bee. Bees with fair to large amounts of pollen showing in their corbiculae were seized with a special bee-catcher (Fig. 2) and destroyed with cyanogas in a few seconds. For each specimen a minimum of nine honey-bees were taken. Since Alfonsus (1933) warns that at times drops of propolis may be mistaken for pollen from a distance all specimens were examined under the microscope and identified as pollen. Under more favorable circumstances fifteen to thirty minutes sufficed to obtain the necessary specimens of an individual plant species. Under less favorable circumstances, due to atmospheric conditions affecting dehiscence of the anthers, a much longer time was needed. Shedding of pollen was heavier in the morning and in the late afternoon. Other insects such as bumble-bees, solitary wasps, flies and countless thrips competed with the honey-bee in gathering or consuming the pollen. During a general

scarcity of the much-needed pollen an occasional bee was found to work from one kind of flower to that of an entirely different species of flower while grathering pollen. Sladin (1912) in England too observed this occasional mixing of pollen by the honey-bee on a single trip. But that is only by way of exception. Bees show great constancy to a particular kind of flower even though a similar species is near at hand.

Anther pollen was generally checked for color in the field, but never in direct sunlight. Pollen masses large enough to conceal a differently colored pollen sac were removed in entirety, checked against the color chart, and the species and color recorded. Several specimens were used in each instance but no variations were noted. It should be noted, however, that Purple Loosestrife is trimorphus and the different length anthers carry different colored pollen. The Wand Lythrum, *Lythrum virgatum*, of the Brooklyn Botanic Garden, had long anthers with Charteuse colored pollen and short anthers with a Chrome Primrose colored pollen. Corbicular pollen of the bees however was all Yew green. Purple Loosestrife, *L. salicaria*, found near Princeton Junction, N. J., however, had long anthers with Bottle green colored pollen and shorter anthers with Chrome Primrose colored pollen. When pollen was scarce or overshadowed by a differently colored pollen sac, an appreciable mass was teased loose and gathered with a probing needle and this mass then checked for color.

The corbicular pollen was checked for color as soon as possible, at least before there was any danger of the pollen becoming "dry." The entire hind leg of the bee

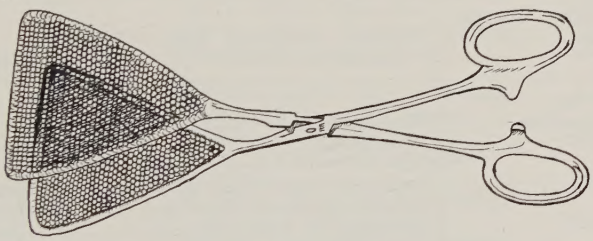

FIG. 2. A bee-catcher. The nine-inch instrument has two triangular spring wire (No. 11 gauge) frames brazed to an arterial clamp. These frames are covered on the outer side with tulle or 13 mesh cotton netting. When closed there is a bee-space (0.25 inch) between the pieces of netting. On smaller flowers the pollen collecting honey-bee and the flower are both grasped together or enclosed between the netted frames, on larger flowers the bee is swept up between the lateral edges of the bee-catcher. The enclosed bee is then held over a cyanogas bottle until destroyed. Between the finger holes is a ratchet locking the device.

was removed, graded for uniformity of color and size of the pollen pellet. With a thumb forceps they were matched for color against the squares of the color charts. The pollen masses were then pried loose from the pollen-basket and rechecked. There was no variation in color as a result. The pollen masses were not, therefore, transparent nor were they influenced by the darker colored tibia of the honey-bee. Some pollen collectors working on a single species of flower showed slightly different colored masses of pollen in the corbiculae, that is, a few would have one color pollen and others a similar or entirely different hue. Parker (1922) also noticed this dissimilarity of color in the pollen masses gathered by the honey-bee from a single species of flower. Thus, he says, bees working on the Box Elder, *Acer negundo*, showed yellow-green corbicular pollen and some showed green pollen. For the Black Maple, *Acer nigra*, some bees had yellow and some had green-yellow pollen. On drying these pollen masses, only one color persisted and under the microscope all the pollen were pure. All "double" colored corbicular pollen reported in Table I was examined by the author and found to be pure.

The results of the Field Methods and the Color Matching are given in Table I. The flowers listed are entomophilous or insect pollinated. The first column lists the color class and approximate wave length in millimicrons, to which is added the specific hue of the anther pollen. The second column lists the plants examined and their scientific names according to the American Joint Committee on Horticultural Nomenclature (1923). The third column shows the color of the same pollen after it was gathered and packed by the honey-bee in its corbiculae. Two colors listed in this third column indicate that about one-half of the pollen collecting bees showed one colored pollen and about one-half showed the other colored pollen in their corbiculae.

TABLE I

FLORA ARRANGED ACCORDING TO THE COLOR OF THE ANTHER POLLEN AND SHOWING THE CHANGE OF COLOR EFFECTED WHEN THE POLLEN IS COLLECTED BY THE HONEY-BEE IN ITS CORBICULAE.

ANTHER POLLEN COLOR. CLASS AND SP. HUE	SPECIMEN	CORBICULAR POLLEN
YELLOWISH RED. 644 mμ		
Cherry red hue	Red Horsechestnut—*Aesculus carnea*	Raisin hue.
Coral red hue	Common Mignonette—*Reseda odorata*	Zanzibar and Rustic brown.
REDDISH RED YELLOW. 614 mμ		
Burnt orange hue	Wallace Dahurian Lily — *Lilium daurianum wallacei*	Chinook hue.
RED YELLOW. 598 mμ		
Bitter sweet orange hue	Horsechestnut—*Aesculus hippocastaneum*	Anatolia.
Cadmium orange	Japanese Rose—*Rosa multiflora*	Henna.
	(Hiawatha Rose—*Rosa* sp.)	Henna.
	(Evangeline Rose—*Rosa* sp.)	Chestnut.
	Yellow Hornpoppy—*Glaucium flavum*	Persian orange (w).
Cadmium yellow	Scotch Broom—*Cytisus scoparius*	Punjab.
YELLOWISH RED YELLOW. 591 mμ		
Deep chrome yellow	Winter Hazel—*Corylopsis spicata*	Raw umber (w).
	Yoshino Cherry—*Prunus yedoensis*	Mandarin orange (w).
	Cherry—*Prunus (mahaleb)*	Tan and Acorn (w).
	Dandelion—*Taraxacum officinale*	Terra cotta and Raw umber (w).
	Miyama Cherry—*Pr. maximowicii*	Cocoa (w).
	Cypress Euphorbia—*Euph. cyparissas*	Caledonian brown (w).
	White Dutch Clover—*Trifolium repens*	Caledonian brown (w).
	Cathay Japanese Rose—*Rosa multiflora cathayensis*	Terra cotta (w).
	Shirley or Corn Poppy—*Papaver rhoes*	Khaki (w).
	Prairie Rose—*Rosa setigera*	Mandarin orange and Tan (w).
	Deutzia sp.—*D. ningpoensis*	Citrine.
	Wichura Rose—*R. wichuraiana*	Chestnut.
	Common Tansy—*Tanacetum vulgare*	Sunstone.
	Shrubby St. Johnswort—*Hypericum prolificum*	Brass.
	Flowering Plum—*Prunus triloba*, var	Bronze.

TABLE I—(*Continued*)

Anther Pollen Color. Class and Sp. Hue	Specimen	Corbicular Pollen
Golden yellow	Service berry—*Amelanchier*	Acorn (w).
	Fr. Hugo Rose—*Rosa hugonis*	Raw umber (w).
	Scotch Rose—*R. spinosissima*	Golden yellow and Khaki (w).
	Altai Scotch R.—*R.* sp. *altaica*	Khaki (w).
	Kansas Plum—*Prunus orthosepala*	Kangaroo.
Jonquil yellow	Roxburgh Rose—*R. roxburghi*	Khaki (w).
Yellow ochre	Flowering Cherry—*Prunus serrulata* var. *Gijo*	Chipmunk and Bronze.
	Fl. Cherry—*Pr. ser.* var. *Amanogawa*	Antique bronze.
Reddish Yellow. 585 mμ		
Light chrome yellow	Wreath Goldenrod—*Solidago caesia*	Whippet.
Lemon chrome yellow	Cornelian Cherry—*Cornus mas*	Yew green (w).
	Winter Honeysuckle—*Lonicera fragrantissima*	Yew green (w).
	Prairie Willow—*Salix humilis*	Olive brown (w).
	Common Box—*Buxus sempervir*	Citrine (w).
	Apple—*Malus sylvestris*	Citrine (w).
	Apple—*Malus sylvestris* (recheck)	Golden yellow.
	Peach—*Amygdalus persica*	Olive brown and Hazel (w).
	Norway Maple—*Acer platanoides*	Acorn and Hazel (w).
	Common Flowering Quince—*Chaenomeles lagenaria*	Lemon chrome (w).
	Bitter Wintercress—*Barbarea vulgaris*	Olive brown (w).
	European Euonymus—*Euonymus europaeus* (Spindlewood)	Mandarin orange (w).
	Morrow Honeysuckle—*Lonicera morrowi*	Khaki (w).
	Lemoine Deutzia—*D. lemoinei*	Citrine (w).
	Sapphireberry Sweetleaf—*Symplocos paniculata*	Raw umber (w).
	Pink Amur Honeysuckle—*Lonicera maacki*	Terra cotta (w).
	Yellow Sweetclover—*Melilotus officinalis*	Auburn and Olive brown (w).
	Roughleaf Dogwood—*Cornus asperifolia*	Serpentine green (w).
	Little Leaf Linden—*Tilia cordata*	Olive brown and Citrine (w).
	White Sweetclover—*Melilotus alba*	Auburn and Hazel (w).
	Canada Goldenrod—*Solidago canadensis*	Whippet.
	Sweet Corn—*Zea mays*	Brass.
	Hupeh Evodia—*Evodia hupehens*	Deep chrome yellow.
	Frost Grape—*Vitis vulpina*	Ivy green.
Sunflower yellow	Common Portulaca—*Portulaca grandiflora*	11 B 12 (Mandarin orange).
	Bushy Aster—*Aster dumosus*	Bronze yellow.
	Willow—*Salix* sp.	Burnished gold.
	Glaucous Willow—*Salix discolor*	Yellow ochre.
	Peony—*Paeonia albiflora* & *P. milkosewitchi*	Tennis and Golden rod yellow.
	Fleabane —*Erigeron flagellaris*	12 J 12 (≈ Tan).

TABLE I—(*Continued*)

Anther Pollen Color. Class and Sp. Hue	Specimen	Corbicular Pollen
9 L 3 (≈ Sunflower y.)	Skydrop Aster—*Aster patens*	Yellow ochre.
	Heath Aster—*A. ericoides*	Burnished gold.
Goldenrod yellow	Floating Heart—*Nymphoides*	Yucatan yellow.
Golden Glow (yellow)	Atlantic Goldenrod—*Solidago arguta.*	11 L 10 (≈ Ponce de Leon yellow).
	St. Bernard Lily—*Anthericum liliago*	Ta Ming.
	White Dutch Clover (recheck)	Antique bronze and 15 J 11 (≈ Whippet).
Chinese yellow	Japanese Pagoda Tree—*Sophora japonica*	Aztec.
9 E 2 (≈ Cream)	Alfalfa—*Medicago sativa*	Khaki.
Pinard yellow	Early Wintercress—*Barbarea praecox*	Olive Green and 14 L 6 (Citrine).
Popcorn yellow	*Narcissus*, var. *Victoria*—Pseudo Narcissus	Rattan.
Chrome lemon yellow	Heartleaf Aster—*Aster cordifolius*	Deep stone.
	Flowering Crab Apple—*Malus bacata.*	13 L 4 (≈ Bistre green).
	Flowering Crab Apple—*Malus atrosanguinea*	Mettalic green.
	Apple—*Malus arnoldiana*	Bistre green.
	Kerria—*Kerria japonica*	Burnished gold.
Colonial yellow	Orpine—*Sedum alboroseum*	13 L 6 (Bistre gr.)
Canary yellow	Welsh Onion—*Allium fistulosum*	Auburn (w).
	Beautyberry—*Calicarpa*	Acorn and Olive brown (w).
Ivory yellow	Eastern Redbud—*Cercis canadensis*	Slate grey and Hazel (w).
	Rugosa Rose—*Rosa rugosa*	Slate grey (w).
	Old-fashioned Weigela—*Weigla florida*	Slate grey and Tan bark (w).
	Medlar—*Mespilus germanica*	Olive brown (w).
	Black Locust—*Robina pseudoacacia*	Auburn (w).
	Fragrant Thimbleberry—*Rubus odoratus*	Yew green and Olive brown (w).
	Hupeh Viburnum—*Vib. hupehense*	Slate grey (w).
	Viburnum—*V. scabrellum*	Hazel (w).
	Kashmir Falsespirea—*Sorbaria aitchisoni*	Slate grey (w).
	Common Buglos—*Anchusa officinalis.*	Auburn.
Yellow. 580 mμ Yellow hue	Purple Loosesrtife—*Lythrum salicaria* (0.5, short anthers)	Autumn.
Chrome primrose yellow	*Forsythia*	Citrine (w).
	Japanese Maple—*Acer palmatum*	Khaki (w).
	Siberian Crabapple—*Malus baccata*	Olive brown (w).
	Threelobe Spirea—*Spirea trilobata*	Olive brown (w).

TABLE I—(*Continued*)

Anther Pollen Color. Class and Sp. Hue	Specimen	Corbicular Pollen
Chrome primrose yellow.....	Fortune Fontanesia—*Fontanesia fortunei*.....	Acorn (w).
	Wolf's Lilac—*Syringia wolfi*.....	Olive brown and Citrine (w).
	Cockspur Hawthorn—*Crataegus crusgali*.....	Citrine (w).
	Japanese Honeylocust—*Gleditsia japonica*.....	Citrine (w).
	American Elder—*Sambucus canadensis*.....	Canary yellow (w).
	Dusty Meadowrue—*Thalictrum glaucum*.....	Pyrethrum yellow (w).
	Ibota Privet—*Ligustrum ibota*.....	Citrine (w).
	Narrowleaf Meadowrue—*Thalictrum lucidum*.....	Olive brown (w).
	Walter Dogwood—*Cornus walteri*....	Citrine (w).
	Largeleaf Dogwood—*C. macrophylla*	Olive brown (w).
	Chinese Chestnut—*Castanea mollissima*.....	Medium chrome green (w).
	Sword Torchlilly—*Kniphofia foliosa*.	Canary yellow (w).
	Wand Lythrum—*Lyth. virgatum* (0.5, short anthers).....	Yew green.
	White Mignonette—*Reseda alba*.....	Olive green.
	Purple Loosestrife—*Lythrum salicaria* (0.5, long anthers).....	Autumn.
Chalcedony yellow.....	Ural Falsespirea—*Sobaria sorbifolia*.	Cub (grey).
	(Tree Falsespirea—*Sorbaria arborea*)	Cub (grey).
Martius yellow.....	Honeysuckle—*Viburnum sieboldi*.....	Olive yellow.
	Evergreen Candytuft—*Iberia sempervirens*.....	14 L 5 (Citrine).
9 K 1 (yellow).....	Viburnum—*V. tomentosum*.....	Canary yellow.
Chartreuse yellow.....	Wand Lythrum—*Lyth. virgatum* (0.5, long anthers).....	Yew green.
Marguerite yellow.....	Thistle—*Cirsium (afrum niveum)*....	13 G. 3 (Olive sheen)
	Climbing Hempweed—*Mikania scandens*.....	13 D 1 (Bronze Clair.)
9 E 1 (yellow).....	*Viburnum Opulus*.....	12 K 4 (Cloudy Amber).
9 F 1 (yellow).....	Jetbead—*Rhodotypus scandens*.....	14 J 2 (Silver Fern).
	Rattlesnake weed—*Hieracum venosum*.....	Yellow ochre.
9 B 1 (yellow).....	Speedwell—*Veronica peduncular*.....	Italian straw.
9 C 1 (≈ Cream).....	Cohosh Bugbane—*Cimicifuga racemosa*.....	Beech.
	Veronida Teucrium—*Rupestris rosea*	12 H 3 (≈ Hay).
9 D 1 (≈ Cream).....	*Rhododendron*.....	12 H 3.
	Arrowwood Viburnum—*Viburnum detatum*.....	13 I 3 (Olive sheen) and 15 J 4 (Olive drab).

TABLE I—(*Continued*)

Anther Pollen Color. Class and Sp. Hue	Specimen	Corbicular Pollen
Greenish Yellow. 572 mμ		
Chrysolite green	Common Pear—*Pyrus communis*	Egyptian Green and Marine green (w).
	Pear—*Pyrus*	Medium chrome green (w).
	Kansas Hawthorne—*Crataegus coccinoides*	Citrine (w).
	Alleghany Blackberry—*Rubus allegheniensis*	Slate grey and Median grey (w)
Yellowish Yellow Green. 568 mμ		
Grass green	Roughseed Clammyweed—*Polanisia trachysperma*	Acorn.
Green. 535mμ		
Bottle green	Purple Lythrum—*Lythrum salicaria*	Gunmetal (Neutral grey and blue red tinge) and Deep chrome green.
Blue Red. 448.5 mμ		
Egg Plant (hue)	Darwin Tulip	56 A 2+ (Kara Dagh)
Plum (hue)	Oriental Poppy	48 E. 12 (Admiral+)
White		
	Persian Nepeta—*Nepeta mussini*	Dark grey (w).
	Prickly Comfrey—*Symphytum asperum*	Slate grey (w).
	Menzies *Spirea*—Sp. *menziesi*	Slate grey (w).
	Common Hoarhound—*Marrubium vulgare*	Smoke brown.
	Cutleaf Chastetree—*Vitex negundo*	Dark grey.
	Persian Centaurea—*C. dealbata*	Hemp.
	Mexican Ageratum—*Ageratum houstonianum*	Dark grey.
	Bluestem Joepye weed—*Eupatorium purpureum*	13 K 5 (≈ Bistre green).
	Scabiosa Centaurea—*C. scabiosa*	12 I 3 (≈ Hay).
	Brownscale Centaurea—*C. jacea*	11 G 3 (≈ Maple).
	Peegee Panicle Hydrangea—*H. paniculata grandiflora*	Medium grey.
	Orange eye Butterflybush—*Buddleia davidi*	Medium grey.
	Panicle Hydrangea—*H. paniculata*	Medium grey.
	Morning Glory—*Convolvulvus major*	Parchment.
	White Snakeroot—*Eupatorium rugosum*	Cub.
	Caraway—*Carum Carvi*	Olive drab.
	Common Thyme—*Thymus serpyllum vulgaris*	Smoke Brown.

TABLE II

SATURATION AND BRILLIANCY OF THE POLLEN LISTED ON TABLE I

VALUES	IN PERCENT	IN UNITS	SATURATION FREQUENCY		BRILLIANCY FREQUENCY	
			Anther	Corbic	Anther	Corbic
Very high plus	93.75%	7.5	1	.....	1	.....
Very high	87.50%	7	19.5	4.5	100.5	2
High plus	81.25%	6.5	1	.....	.....	.....
High	75 %	6	43	15.2	19.5	18.7
Medium plus	62.50%	5	.....	.....	1	1
Medium	50 %	4	41	47.8	4	55.3
Low plus	37.50%	3	.....	1	.....	1
Low	25 %	2	16.5	54	1	49
Very low	12.50%	1	5	4.5	2	2
			127	127	129	129

The 17 white or achromatic anther pollens are not included in the above listing.

OBSERVATIONS

Of the 146 anther pollens checked, 129 (88.3%) are colored or chromatic. 17 anther pollens were found to be white or achromatic. The samples were taken entirely at random; either as the different flowers were available in one locality or as they blossomed during the course of the two summers in 1944 and 1945. Of the colored anther pollens 57 are reddish yellow, 33 are of a yellow color and 23 are yellowish red yellow. Only 1.5 anther pollens remained unchanged in hue after being gathered by the honey-bee. One was the Common Flowering Quince, having a Lemon Chrome yellow anther pollen and it retained that color in the bees corbiculae. One-half of the bees working on the Scotch Rose, having a Golden yellow anther pollen, had corbicular pollen of that hue, the others showed Khaki colored pollen in the corbiculae. The change was due to a decrease from high saturation and brilliancy to medium saturation and brilliancy.

37.2 other anther pollens did not change in color class, but did change (increase or decrease) in saturation and nearly all of these decreased in brilliancy. All the rest, 107.3 (73%) changed in color class, in most cases also in saturation and brilliancy.

Where two colors are reported in the corbiculae of the honey-bee working on a single species of flower, these colors were often closely related. Thus Zanzibar and Rustic brown, Slate grey and Hazel, Slate grey and Tan bark differed between themselves only in saturation. Golden yellow and Khaki, Auburn and Hazel differed only in saturation and in brilliancy, but not in color class. Other double colors differed in class and sometimes in saturation and in brilliancy.

Among the corbicular pollen colors, 28 are yellow red, 25.8 are yellowish red yellow, 36.2 are reddish yellow, and 15 are yellow.

The anther pollen hues have a Mean wave length of 585.3 mμ and the corbicular pollen hues one of 588.8 mμ. These Means were calculated from 125 variates in each series. The pollen of the Red Horse chestnut, of the Darwin Tulip, of the Oriental Poppy, change to non-spectral hues in the honey-bee's corbiculae, and one-half of the Alleghany Blackberry pollen and one-half of the Purple Lythrum pollen turn grey, while the 17 white anther pollens are achromatic. Hence these 21 variates were disregarded in the calculations. The standard deviation or amount of variability in each series is given in Table III. The coefficients of variation (Table III) show that the corbicular pollen hues are dispersed more round their Mean than are the anther pollen hues.

The difference between the Mean wave lengths is 3.5 mμ. This is significant according to Fisher's (1934) standard, $D > 2 \times E_D$, where D is the difference between the Means, and E_D is the standard error of the difference. That is it is significant if it is greater than twice its standard error. The standard error of the

TABLE III

Coefficients of Correlation Between Anther Pollen and Corbicular Pollen Hues and Other Factors, With Their Probable Error (±), Their Mean Value (M), Standard Deviation (σ), and Coefficients of Variation (c. v.).

	Anther Pollen Hues	Anther Pollen Saturation	Anther Pollen Brilliancy	Corbicular Pollen Hues	Corbicular Pollen Saturation	Corbicular Pollen Brilliancy	
Anther pollen hues.		+0.4498 ±0.0481 t =6.253	−0.0322 ±0.0586 t =0.359	+0.5795 ±0.0400 t =7.887	+0.1792 ±0.0583 t =2.020	−0.1246 ±0.0589 t =1.410	M = 585.3 mμ σ = 8.49 c. v. = 1.45%
Anther pollen saturation.	+0.4498 ±0.0481 t =6.253		+0.0965 ±0.0588 t =1.095	+0.3170 ±0.0542 t =3.708	+0.4080 ±0.0500 t =4.976	−0.0697 ±0.0591 t =0.788	M = 4.8 (60%) σ = 1.75 c. v. = 36.40%
Anther pollen brilliancy.	−0.0322 ±0.0586 t =0.359	+0.0965 ±0.0588 t =1.095		−0.1045 +0.0596 t =1.166	+0.1118 ±0.0591 t =1.256	+0.3134 ±0.0535 t =3.719	M = 6.7 (83.75%) σ = 0.76 c. v. = 11.38%
Corbicular pollen hues.	+0.5795 ±0.0400 t =7.887	+0.3170 ±0.0542 t =3.708	−0.1045 ±0.0596 t =1.166		+0.3610 ±0.0524 t =4.604	+0.0959 ±0.0597 t =1.068	M =588.8 mμ σ = 12.37 c. v. = 2.11%
Corbicular pollen saturation	+0.1792 ±0.0583 t =2.020	+0.4080 ±0.0500 t =4.976	+0.1118 ±0.0591 t =1.256	+0.3610 ±0.0524 t =4.604		+0.5249 +0.0435 t =6.867	M = 3.4 (42.5%) σ = 1.57 c. v. = 46.29%
Corbicular pollen brilliancy.	−0.1246 ±0.0589 t =1.410	−0.0697 ±0.0591 t =0.788	+0.3134 ±0.0535 t =3.719	+0.0959 ±0.0597 t =1.068	+0.5249 ±0.0435 t =6.867		M = 3.5 (43.75%) σ = 1.46 c. v. = 41.19%

difference (E_D) between the Mean pollen hues is 1.34. This was calculated from Paterson's (1939) formula: $E_D = \sqrt{E_A^2 + E_B^2}$, where E_A equals the standard error $\left(\frac{\sigma}{\sqrt{\eta}}\right)$ of one quantity and E_B equals the standard error of the other quantity. From the above it is evident that the difference between the Mean pollen hues is significant. Fisher's statistical "t" test gives the same result. The difference is significant if $D > t \times E_D$. According to the Table of "t," in this instance its value is 1.95 times the error of the difference 1.34 equals 2.61. The difference 3.5 in mμ exceeds it and is therefore significant.

Saturation calculations do not include the white anther pollens as they are without this attribute. 41.2 anther pollens do not decrease in saturation. 12.5 anther pollens increase their hue saturation when collected by the honey-bee. About 57% of the anther pollens decrease in saturation or become "greyer." The lower saturated anther colors show the greater change in saturation.

Mean anther pollen hue saturation is 4.8 (or 60.3%) and for corbicular pollen hues is 3.3 (or 42.4%), the difference being 1.5 (or 18.7%). This difference is greater than twice its standard error (0.20, from Paterson's formula above) and it therefore significant. Applying the "t" test gives the same result. 1.5 > 1.96 (t) x 0.20 equals 0.39.

Only 4.5 anther pollen hues do not decrease in brilliancy. The highly brilliant hues show the greater change in brilliancy.

Mean anther pollen brilliancy, exclusive of the 17 white anther pollen samples, is 6.7 (or 83.7%) and the Mean corbicular pollen hue brilliancy is 3.5 (or 44.5%) a difference of 3.2 (or 40%). This difference greatly exceeds the value of twice its standard error, which latter is 0.14 (from Paterson's formula) and it is therefore significant. The "t" test gives the same result, and Fisher's statistical "F" and "z" tests confirm the above calculations.

Table III gives the values used in the preceding paragraphs, but not the standard error of the difference (E_D) which must be calculated separately from the formula of Paterson given above. The coefficients of variation (c. v.) are however given. These express in percentages the dispersion of the variates around their respective means (M). The unit and decimal values for anther and corbicular pollen hue saturation and brilliancy are interchangeable with percentage values. 1 equals 12.5%, 2 equals 25%, etc. The results will be the same.

Table III also gives the coefficients of correlation (r) between anther and corbicular hues, saturation and brilliancy values. It is understood that the reaction between the given associated variables is not mutual. Anther pollen color constants are in this study the independent factors and corbicular pollen color constants are the dependent factors.

Yule (1919) says that if the coefficient of correlation exceeds four times its probable error it is significant, otherwise its importance is primarily to show positive or negative relationship. The probable errors (following the ± sign) given in Table III were calculated from Peter & Van Voorhis' (1940) formula:

$$PE_r—0.67449\ \frac{1—r^2}{\sqrt{n}}$$

where "r" of course is the coefficient of correlation and "n" the number of variates.

The more modern and critical "t" might also be used to confirm the significance of the correlation coefficients evaluated. The formula used to calculate the values of "t" are from Paterson (1939);

$$\text{'t'} = \frac{r \times \sqrt{n—2}}{\sqrt{1—r^2}}$$

The "t" values are given in Table III following the probable error of the coefficients of variation. From a table of "t" values it will be evident that any such value exceeding 1.959 is significant.

In every instance the anther pollen color constants show their significant influence upon the corresponding corbicular pollen color constants, the latter being the dependent factors. It will also be noticed that saturation values are closely associated with their respective hue values, but brilliancy values are correspondingly independent. Since such is the case, and the decrease in brilliancy from the anther pollen to the corbicular pollen is 40% it seems quite certain that this is the most important factor in effecting the change of color.

CONCLUSIONS

It is not by mere chance that the color changes when anther pollen is gathered by the honey-bee and packed in its corbiculae. The discussion of probable causes for this change is inferential and direct proof is not attempted.

Brilliancy is the lesser correlated factor in regard to hue and yet shows more than twice (40%) as much change as does saturation (18.7%) from the anthers to the corbiculae. Here seems to be the reason for the change of color. The decrease in brilliancy is due to a change in the surface texture of the pollen mass when it is removed from the anthers and formed into pellets in the corbiculae of the honey-bee. Pollen grains are quite freely and loosley attached to the anthers and present *en massé*, a sufficiently rough surface to cause a diffuse reflection of the incident

light and consequently affect to a lesser degree the wave lengths which produce the color sensations. When these same pollen grains are gathered by the honey-bee they are compressed by the auricle on the anterior end of the planta of the hind leg of the bee and thus squeezed upward into the pollen basket or corbicula to form the pollen pellet or corbicular pollen mass. In the process of packing the bee also uses the middle legs to pat down the pellets thus formed and render them more compact. This relatively smoother mass surface reduces the diffuse reflection of light and hence alters to a degree in spectral composition the light waves that produce the color sensations. This may be illustrated by comparing the pollen grains to freshly fallen snow. Pollen grains are to a great extent as transparent as ice-crystals and otherwise vie in beauty by their sculpturing with the myriad forms of snowflakes. Freshly fallen snow is a diffuse reflector of light, but when it is trodden down or a crust forms over it this property of reflection is reduced. In like manner when pollen is packed by the bee in the corbiculae it looses much of its brilliancy.

Another reason for the change of color is the addition of moisture to the pollen when it is taken from the anthers of the flowers and packed in the corbiculae. Parker (1922) notes this factor when he says that pollen of two different colors was collected from bees working on the Acer negundo, "but upon drying these (i. e., pollen masses) only one color was persistent." In the pollen packing process very little pollen reaches the corbiculae without becoming thoroughly moist and sometimes the pollen masses are fairly liquid with moisture. This addition of moisture, mostly honey, dulls still further the natural brilliancy of the anther pollen, hence the corbicular pollen masses often appear as if "water-logged." According to Todd and Bretherick's (1942) analysis, corbicular pollen contains a mean 11.6% of water while hand collected, i. e., anther pollen has a mean 9.72% water content. Vivino and Palmer (1944) give a mean 23.89% moisture value for corbicular pollen after partial drying for 24 hours. Todd and Bretherick (1942) also note the presence of water-soluble (and fat-soluble) types of pigments in pollen. Any addition therefore of moisture to anther pollen during the transfer to the corbiculae would naturally tend to dilute the pigment and change the color. Chemical analysis indicates that honey is predominantly used for this moistening function and hence honey solids and water content increase disproportionately in corbicular pollen.

Phillips (1929) showed that even water-white honey absorbs some of the light waves, in the following amounts: blue light, 36%, yellow-green light, 23% and red light 18.5%. Even though the honey-bee uses a comparatively small amount of honey in the pollen packing process this fluid coating on the pollen grains absorbs some of the light waves, twice as much blue as red, and one and one-half as much yellow-green as red. This might account for a slight shift of the mean anther hue of the pollen from the 585.3 mμ toward the reddish end of the color spectrum, or toward the mean corbicular hue of 588.8 mμ.

Since the ether extract in pollen may also contain pigments, its decrease would effect a change of color. Todd and Bretherick (1942) give evidence of this decrease. Hand collected, i. e., anther pollen contains a mean 5.01% ether extract while corbicular pollen contains a mean 4.96% ether extract.

Another factor may be the addition of foreign matter to the corbicular pollen masses in the process of packing by the not always fastidious honey-bee. Corbicular pollen masses under the microscope show bits of fiber, dust, gritty matter resembling tiny particles of coal-like mineral matter, that do not stain and are impervious to the point of a probing needle. Some of these minutiae were estimated at from 200 or more microns in length or breath. Pollen grains range in size from 4.5 microns, the smallest (Forget-me-not) to 200 microns in diameter for the largest (Pumkin). In the corbicular pollen of the White Sweet Clover distinctive lighter colored "flakes" appeared but the effect in this case was to

"lighten" the pollen pellets. No count was made of this foreign matter nor was it identified, but its presence generally tends to darken the corbicular pollen masses. While anther pollen is also exposed to contamination from dust in the air, soil, etc., the probability for greater contamination is increased for the honey-bee due to its greater range, its flight activity from flower to flower, and its hairy body serving as a "catch all" for such foreign particles.

SUMMARY

Pollen literature ignores to a great extent the important factor of color. In bee literature seldom is a distinction made between anther and corbicular pollen when speaking of the color of pollen.

Introspectively defined colors may be translated into mathematical terms, by the use of color constants and approximate wave lengths may be assigned to practically all hues. Using a standard color chart, anther and corbicular pollen may be identified by color-matching.

Two seasons' field work show for the 146 specimens examined about ten general classes of color, as yellowish red, red yellow, yellow, greenish yellow, etc., and about one hundred distinct hues as, Cherry red, Coral red, Henna, Rustic brown, etc. Most anther pollens (88.3%) are colored chromatically, the rest are white. Only 1.5 pollens were observed to remain unchanged in color when packed by the honey-bee in its corbiculae. Changes in color may be due to decrease in saturation or a decrease in brilliancy or both, and the changes are significant.

Saturation is closely correlated with its associated hue but brilliancy enjoys greater freedom. Corbicular pollen color constants are the dependent factors in relation to anther pollen color constants, but preserve among themselves the same relationship as do the anther pollen color constants.

Brilliancy's decrease is the important factor in the change of color between anther and corbicular pollen. The decrease is caused by a change of surface texture in the pollen masses, the addition of moisture, absorption of light waves by the honey used in packing the pollen, dilution of water-soluble pigments and the addition of foreign matter. Hence corbicular pollen differs in color from its corresponding anther pollen.

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A SYSTEMATIC STUDY OF THE MAIN ARTERIES IN THE REGION OF THE HEART—AVES XVI

Charadriiformes. Part 1[1]

FRED H. GLENNY[2]

As in previous studies on the main arteries in the neck and thorax of birds, the writer herein presents the basic arrangement-pattern of these vessels in six species of Charadriiformes.

The patterns of arteries—derivatives of the embryonic aortic arches and other embryonic vessels of the head and neck region—appear to be significant as evidence in relative degrees of relationships among birds. It may be pointed out that orders, families, and genera with wide differences in the arrangement-patterns may be presumed to be widely divergent in their evolution, whereas those orders or families with uniform or highly similar arrangement-patterns appear to represent groups in which evolution may be regarded as centralized, terminal, or parallel in nature.

MATERIALS

Single specimens of the following species were dissected and diagrams of the arteries in the neck and thorax prepared:

Charadriidae:
Oxyechus v. vociferus.
Scolopacidae:
Actitis macularia.....#225065 USNM
Macrorhamphus griseus.
Philohela minor.
Pisobia minutilla.....#223691 USNM
Laridae:
Larus argentatus.

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Materials for this study were collected by the Division of Birds, United States National Museum, Division of Ornithology, Cleveland Museum of Natural History, Division of Ornithology, Royal Ontario Museum of Zoology, and the writer.

OBSERVATIONS

The basic ordinal arterial arrangement-pattern is characteristic for the species studied.

The innominate artery (2) divides to form the common carotid (8) and subclavian (9) arteries. The latter then gives rise to the coracoid major (10), axillary (11), intercostal (12), and two pectoral (13) arteries in order, while the common carotid gives rise to the thyroid artery (16) and ductus shawi (14) before giving rise to the cervico-vertebral (17) and internal carotid (trunk) (21) arteries. The syringo-tracheal artery (15) arises from the ductus shawi; a short basi-oesophageal

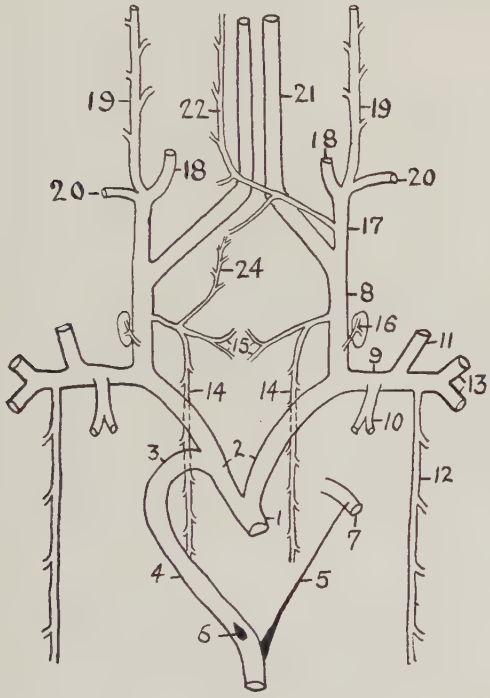

FIG. 1

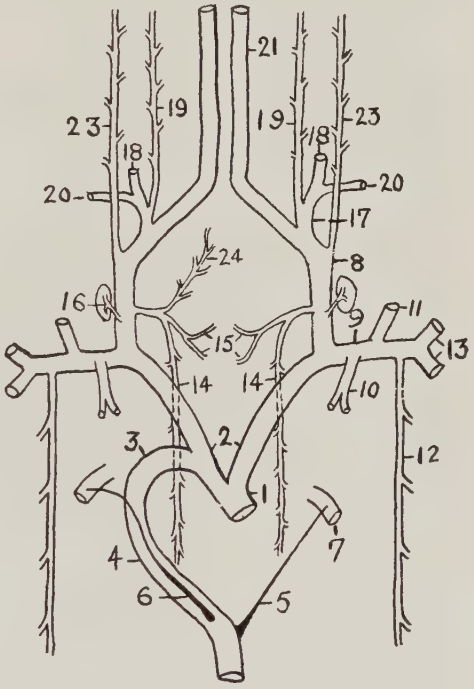

FIG. 2

FIG. 1. Diagram of main arteries of neck and thorax of *Oxyechus v. vociferus*. Ventral view.
FIG. 2. Diagram of main arteries of neck and thorax of *Larus argentatus*. Ventral view.

KEY TO ABBREVIATIONS

1. aortic root.
2. innominate arteries.
3. right systemic (4th aortic) arch.
4. right radix aortae.
5. ligamentum aortae.
6. ligamentum botalli.
7. pulmonary artery.
8. common carotid artery.
9. subclavian artery.
10. coracoid major artery.
11. axillary artery.
12. intercostal artery.
13. pectoral arteries.
14. ductus shawi.
15. syringo-tracheal arteries.
16. thyroid artery.
17. cervico-vertebral artery.
18. vertebral artery.
19. superficial cervical artery.
20. scapular artery.
21. internal carotid (trunk) artery.
22. accessory oesophageal artery.
23. accessory superficial cervical artery.
24. basi-oesophageal artery.

artery (24) arises from the right ductus shawi. The scapular artery (20) arises variously from the cervico-vertebral artery. The ligamentum aortae (5) is present, while the right ligamentum botalli (6) may be present or atrophied in various degrees.

The Charadriiformes are "aves bicarotidinae normales" and both internal carotid (trunk) arteries enter the hypapophysial canal before passing anteriorly to the head.

The right superficial cervical artery (19) normally serves as the ascending-oesophageal artery.

In *Oxyechus vociferus vociferus* (Figure 1) the superficial cervical (19), vertebral (18), and scapular (20) arteries arise from the cervico-vertebral artery (17). An accessory oesophageal artery (22) arises from the left cervico-vertebral artery and passes diagonally across the ventral surface of the neck until it comes to the left side of the oesophagus and then passes anteriorly along its surface. The ligamentum botalli (6) remains as a small "button" at the site of its distal attachment to the right radix aortae (4).

In addition to the basic ordinal pattern, *Larus argentatus* (Figure 2) presents an accessory superficial cervical artery (23) on both left and right sides of the neck. This artery arises from the common carotid just posterior to the origin of the cervico-vertebral artery, and lies more ventral than does the normal superficial cervical (19). In addition to the ligamentum aortae (5), the right ligamentum botalli (6) is present and prominent and maintains both proximal and distal attachments.

Macrorhamphus griseus and *Actitis macularia* are very similar to *Oxyechus v. vociferus* except that (a) there is no noticeable accessory-oesophageal artery (22), (b) the vertebral artery (18) arises nearer the base of the cervico-vertebral artery (17) and (c) the ligamentum botalli (6) is entirely present.

Philohela minor is like *Macrorhamphus griseus* except that the ligamentum botalli appears to be fused with the right radix aortae or completely atrophied.

In *Pisobia minutilla*, the arrangement is the same as that of *Macrorhamphus* except that an accessory superficial cervical, more ventral than the normal superficial cervical, arises from the cervico-vertebral artery on the right side. Both the normal and accessory right superficial cervicals send blood to the oesophagus. The ligamentum botalli is present and complete.

DISCUSSION

From the above observations, it may be seen that although there is a basic ordinal arrangement-pattern of arteries in the neck and thorax of the Charadriiformes, there are also family, as well as individual or specific, variations. This would seem to indicate that the order is fairly well established with respect to evolutionary trends. The various families, however, do not appear to represent terminal forms. This is illustrated in the different families which present patterns somewhat divergent in nature.

The various species, and even families, of this order of birds show relatively less divergence, however, than do many of the species and even families of other orders of birds—Coraciiformes, Anseriformes, and Galliformes (Glenny 1943, 1944, and unpublished papers).

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HOLOCHOANITES ARE ENDOCEROIDS

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INTRODUCTION

The Holochoanites may be defined as those cephalopods in which the septal necks are so elongated that they extend from the septum of which they are a part and a prolongation, apicad to the next septum, or even farther. Hyatt (1884) first regarded the Holochoanoidea as one of two major divisions of the Nautiloidea. Later (1900) he replaced his other division, the Ellipochoanoidea, by four divisions the Orthochaonites, Cyrtochoanites, Schistochoanites and Mixochoanites, and changed the name Holochoanoidea to Holochoanites for uniformity. In the meantime, further study caused him to modify the contents of the holochoanitic division materially. Some genera originally placed in this group, such as *Trocholites*, proved upon further study to possess ellipochoanitic septal necks. The genus *Aturia*, while properly holochoanitic, was removed because it was recognized that it represented a development of elongated septal necks in Tertiary time, which was obviously quite unrelated to that of other holochoanitic cephalopods, few of which survived the close of the Ordovician. Miller and Thompson (1937) showed that the elongation of the septal necks in *Aturia* was a secondary feature and the ellipochoanitic ancestry was indicated by the retention of connecting rings. It was believed that the Holochaonites proper contain cephalopods in which the long necks were primitive, and no connecting rings were developed.

Unfortunately Hyatt does not seem to have committed himself on his ideas concerning the relationship of the Holochoanites with other cephalopods. It is not clear whether this was because of his preoccupation with the phyletic significance of early stages and the controversy that developed about the origin of the Ammonoidea and their relationship to the Nautiloidea, or whether he was as much perplexed by the problem as have been those of us who have come after him in the study of cephalopods. Two lines of evidence seemed at the time to suggest the primitive nature of the Holochoanites. First, the true holochoanitic cephalopods appeared to be concentrated at the bottom of the Paleozoic; only a few discouraged types managed to continue after the close of the Ordovician. Second, a morphological comparison seemed to indicate that a siphuncle wall composed of a single structure, the septal neck, was logically simpler and more primitive than one in which the neck was short and was supplemented by a connecting ring. Indeed, the belief was once suggested that the connecting ring developed as a differentiation of a part of the septal neck. Ruedemann (1905) suggested a possible transition from the holochoanitic to the ellipochoanitic condition by shortening of the septal neck and development of the connecting ring from the endosipholining.

Thin section investigation, however, has presented evidence that holochoanitic structure is not primitive, but that the Ordovician holochoanites developed from ellipochoanitic cephalopods, and retain connecting rings as evidence of their ancestry (Flower, 1941).

The term endoceroid has been variously, and sometimes loosely used but is probably best restricted to cephalopods with relatively large and tubular siphuncles, the interiors of which are occupied by endocones (Flower, 1941). As thus defined it excludes the Ellesmeroceratidae which lack endocones, although from the superficial similarity of the siphuncle wall of *Ellesmeroceras* and true endoceroids, that genus has been considered as an endoceroid by more than one student of the group.

Hyatt (1900) erected the Endoceratida, which has essentially the scope of our Endoceroidea, as a division of the Holochoanites. He regarded it as essentially holochoanitic, a conclusion which it is necessary now to dispute, and suggested that the group might contain cephalopods without organic deposits in the siphuncle. All genera placed in the Endoceratida, however, do contain endocones. Ruedemann (1906) in reporting holochoanitic structure in *Cyclostomiceras* and *Protocycloceras*, believed that they were primitive in this respect, but did not transfer them to the Holochoanites as would appear necessary by definition.

More recent studies have shown that holochoanitic structure is not as widespread as was formerly supposed. Foerste's earlier papers contain many allusions to supposedly widespread holochoanitic siphuncles in pre-Chazyan cephalopods. Several times he asserted the belief that all Canadian and Ozarkian cephalopods were holochoanitic, and on the strength of this premise erected at least one new genus, *Levisoceras*, which he separated as an Ozarkian holochoanitic shell from the ellipochoanitic *Cyrtocerina* of the Ordovician. Further investigations caused him to reject this hypothesis. However, it is a fact that the siphuncle walls of these older cephalopods are often thicker and are more persistently preserved than are those of their younger relatives, and anyone who has seen Tarphyceratidae with a series of camerae completely destroyed except for the siphuncle, can readily understand how Foerste supposed such siphuncles to be composed of the relatively strong septal necks instead of the connecting rings, which in younger cephalopods are often fragile, so fragile indeed that they are often wanting. Indeed, they are practically unknown in some genera, as in *Leurocycloceras* and the Silurian species assigned to *Heracloceras*.

Kobayashi (1935, 1935A, 1936) in a study primarily based upon new morphological evidence supplied by Asiatic cephalopods, found that some shells which are typical endoceroids, as defined above, were not holochoanitic. He proposed a phyletic scheme (Kobayashi, 1935, p. 750) which involved first of all the concept that the endoceroid was not primitive, but was highly specialized. He regarded holochoanitic structure as a specialization, but an early specialization, and interpreted his ellipochoanitic endoceroids as individual departures from a dominantly holochoanitic stock. He regards the Plectronocertaidae as possessing unstable siphuncles which vary from cyrtochoanitic to orthochoanitic. He regards his family Ellesmeroceratidae, however, as varying from holocohanitic in *Ellesmeroceras* to ellipochoanitic in *Clarkeoceras*. The line containing the ellesmeroceroids, the piloceroids and endoceroids, is regarded as dominantly holochoanitic. At three points, the Chilioceratidae, Baltoceratidae and Troedssonellidae, independent transitions from holochoanitic to ellipochoanitic siphuncles are potsulated. A second main line is of somewhat less definite origin. In his diagram, Kobayashi traces it to an unknown ancestor of the Plectronoceratidae but, in his text, notes that it may also have come from the Ellesmeroceratidae. He regards this line as primitively holochoanitic for, branching from it, he places the supposedly holochoanitic Protocycloceratidae and Wolungoceratidae, prior to the point at which he indicates a transition from holochoanitic to ellipochoanitic structure. Beyond this point the line splits producing the orthochoanitic "Orthoceratidae" on one hand and the cyrtochoanitic "Actinoceratidae" on the other.

Of the Protocycloceratidae Kobayashi says: "On the other hand I am inclined to recognize that *Protocycloceras* or *Orygoceras* is a Clycloderatidae or an Orthoceratidae with a holochoanitic siphuncle in which the evolution in reference to the septal character is retarded."

Later investigations support Kobayashi's main thesis of the specialized nature of the Holochoanites but show that they are even more restricted than Kobayashi believed at that time.

Schindewolf (1942) has presented a general concept of nautiloid development which is unfortunately characterized by rather vague definitions of the groups

concerned. This has previously been discussed by the writer (Flower, 1946, p. 72). Recently much new information on the older cephalopods has been presented, (Ulrich, Foerste, Miller and Furnish, 1942; Ulrich, Foerste and Miller, 1943; Ulrich, Foerste, Miller and Unklesbay, 1944) but the chert which replaced the substance forming the bulk of the material was not suitable for close morphological study, and the classification is rather generalized, the advances in knowledge of the structure are not great, and little attention is given to the important problems of phylogeny. (See Flower, 1946, p. 73–74).

Investigations on the part of the writer showed that much new information awaited discovery in the siphuncle walls of these older cephalopods. The more important of these results were published (Flower, 1941, 1941a), but much information was omitted as seemingly irrelevant. Thin section study showed that many of the supposedly holochoanitic cephalopods possessed instead ellipochoanitic siphuncles. This is true of the supposedly holochoanitic *Protocycloceras*, *Baltoceras*, *Ellesmeroceras* and *Proterocameroceras*. The evidence of the sections then at hand indicated that many, perhaps most pre-Chazyan cephalopods which were supposedly holochoanitic had instead short septal necks supplemented by connecting rings which were thick enough that they resembled septal necks to a very deceptive extent in opaque sections. Thin sections of well preserved material would show the difference at once. Further, it was found that the connecting rings were often not homogeneous, but developed either a pattern of different layers, or a pattern in which dense and apparently amorphous material termed the eyelet, tended to concentrate in the tip of the ring. The beginning of holochoanitic structure was not definitely placed, but study of Ordovician endoceroids indicated that (1) no longiconic endoceroids prior to the Chazyan possessed good evidence of holochoanitic structure, (2) the holochoanitic septal necks of Chazyan and younger endoceroids were supplemented by a connecting ring which usually agreed with that found in many Canadian ellipochoanitic cephalopods in possessing an eyelet. From these facts it was concluded that the holochoanitic endoceroids developed from ellipochoanitic types which reached their acme in the Canadian, and that the retention of the connecting ring was clear evidence of their ellipochoanitic ancestry. Further investigation indicated strongly that the ellipochoanitic ancestors were properly endoceroids, and that neither the older endoceroids nor their ancestors, the ellesmeroceroids achieved necks long enough to be considered properly holochoanitic. Additional evidence has led to the present statement of these conclusions in the more forceful terms embodied in the title of the present work, and has made possible the presentation of more evidence and the tracing of the phylogeny in more detail than the earlier evidence warranted. The earlier conclusions of the writer (Flower, 1941) were necessarily presented in somewhat general terms. A later brief statement of the phylogeny was included in the introductory portion of the study of the Cincinnatian cephalopods (Flower, 1946, p. 74–90), but the intention of this exposition was to present the evolutionary background of the Upper Ordovician cephalopod faunas, and most of the new evidence bearing upon the problem was passed over or stated only briefly.

PHYLOGENY

The oldest cephalopods comprise the endogastric cyrtocones of the Plectronoceratidae which grade without any precise boundary into the orthoconic cephalopods of the Ellesmeroceratidae. While many genera and species are now known, due to the work of Kobayashi in Asia, and to Ulrich, Foerste and Miller (1942), Ulrich, Foerste, Miller and Unklesbay (1944) in America, details of internal structure are known from only a very few of the specimens. Most of the American material consists of chert internal molds and replacements which are not suitable for a proper morphological study. Some, but plainly not all, of the members of this group possess diaphragms, but it is to be feared that some of the structures

termed pseudodiaphragms are not natural but are either adventitious structures or the appearance presented by the rather thick connecting rings in sections which approach close enough to the wall of the siphuncle to intersect it tangentially. These cephalopods have septal necks which are ellipochoanitic or often aneuchoanitic, that is, possessing septa which are scarcely bent apicad at the point where they meet the connecting rings. Study of a considerable suite of specimens has led the writer to reject the holochoanitic siphuncle wall and the presence of diaphragms which Kobayashi (1935a, p. 22, Fig. II), represents for the Ellesmeroceratidae.

The next step in development is that represented by the Proterocameroceratidae (Flower, 1946, p. 80). The siphuncle wall may be as primitive as that of the Ellesmeroceratidae, but within the siphuncle are developed endocones, making these cephalopods true endoceroids. Much variation has been noted in the length of the septal necks in this group; Necks vary from those which are aneuchoanitic to those which approach but do not quite attain the holochoanitic pattern. Likewise, there is here variation between the banded type of connecting ring and that showing the eyelet, with important transitional stages showing the close relationship of these seemingly opposed structural types. There is likewise variation in the form of the endosiphuncle, which may be simple, as appears to be the rule among the Middle Canadian types, or may become quite complex as in the Upper Canadian *Proterocameroceras* or the sole Chazyan member of the stock, *Meniscoceras*.

The next stage in advancement is marked by two contemporaneous modifications, first an elongation of the septal necks until a holochoanitic condition is reached, and second, a tendency for both the shell and the siphuncle to expand very rapidly, although this may be followed in the mature shell by a living chamber which is more or less contracted, so that a typical breviconic shell is eventually formed. This change has reached its acme in the true Piloceratidae. It is believed that some of the Asiatic piloceroid shells may supply a transition from the Proterocameroceratidae to the Piloceratidae in respect to both of these important features. Certainly some of these shells, as *Coreanoceras* and *Manchuroceras*, are only moderately breviconic. Further, it is just among these forms which are transitional in regard to the shell form, in which the rate of expansion of the conch is mainly concerned, that one finds the ellipochoanitic siphuncles. However, Kobayashi has described structures in the endosiphuncles of these cephalopods which indicate that they have undergone very marked specializations of their own. Admittedly, a number of these cephlaopods require further study before their precise position in the phyletic scheme can be definitely established.

At the close of the Canadian the Piloceratidae disappear and the Proterocameroceratidae are represented only by one genus, *Meniscoceras* which penetrates as high as the Middle Chazyan. Their place is taken by slender endoceroids which are regarded as descendants of the Piloceratidae, from which they inherit a tendency for the siphuncle to expand markedly in the early growth stages so that it may occupy the entire apex of the shell, and holochoanitic septal necks which still retain connecting rings. The combination of a slender shell and holochoanitic septal necks has been used as the criterion for the family Endoceratidae. The writer previously believed that some members of this family lost the connecting ring which was retained in the more generalized endoceroids. Further examination of thin sections has, however, indicated that the loss of the connecting ring in those specimens which lack it is more probably the result of solution under unfavorable conditions of preservation. The Piloceratidae-Endoceratidae series is essentially a tachygenetic sequence. Reduce the pattern of a piloceroid phragmocone in size, add to the end a shell in which the siphuncle and conch are both slender, and the resultant type is essentially a *Nanno*, such as persists from the Chazyan to the Richmond. Reduction of the recapitulatory swollen siphuncle of a *Nanno* results first in the inflated, but still swollen, siphuncle of a *Suecoceras*, and finally in the tubular siphuncles found in those cephalopods to which the generic names *Cameroceras* and *Foerstella* have been applied.

THE ELLESMEROCEROID COMPLEX

It is necessary to begin the detailed tracing of structural changes with a survey of the ellesmeroceroids, which are properly the ancestors of the endoceroids.

The ellesmeroceroids are primitive cephalopods which were the dominant and perhaps the exclusive representatives of the nautiloids up to the close of the Lower Canadian (Gasconade, Wanwanian), only a few genera and species surviving into later faunas. Although exceedingly variable in form, these cephalopods are readily recognized by their small size, very closely spaced septa, the dominantly compressed section, the attendant development of lateral lobes of the sutures, and the large ventral siphuncle which is devoid of endocones. Much remains to be learned concerning the crucial morphological features of these cephalopods, but many species have been described (Kobayashi, 1933, Ulrich, Foerste and Miller, 1943; Ulrich, Foerste, Miller and Unklesbay, 1944).

Shells of this group exhibit almost every gradation in form from strongly curved endogastric cyrtoceracones to orthoceracones. The shells likewise show all gradations between those which expand very rapidly to those which are essentially tubular. The mature living chamber and apertures may be simple, or may be variously constricted and contracted. The extreme of contraction is reached in *Buehleroceras* and *Burenoceras*, which develop apertures strongly suggestive of the younger *Phragmoceras*. The section is dominantly compressed, often strongly so. However, some species of *Ellesmeroceras* are circular in section, and *Pachendoceras* is probably a depressed ellesmeroceroid rather than an endoceroid. The two supposed spicula which have been figured in this genus are open to other interpretations. One is probably adventitious (Ulrich, Foerste, Miller and Unklesbay, 1944, Pl. 64, Fig. 1), and the other (Ibid., Pl. 61, Fig. 4), represents instead the apex of the siphuncle. The sutures may be essentially transverse or may be inclined orad on the dorsal (antisiphonal) side. Lateral lobes are commonly developed, but all gradations between straight and deeply lobed sutures occur, the variation generally corresponding to the development of a compressed cross section.

In spite of wide form variation, the group is a homogeneous one. Many of the species lie so close to the boundaries of the genera as at present defined, that their reference to either one to the exclusion of the other is sometimes extremely difficult. While taxonomic difficulties may easily result, it is clear that the ellesmeroceroids represent a homogeneous but exceedingly plastic group, and one which expanded rapidly in the early Canadian, possibly because it lacked ecological competition.

Attempts to express the diversity exhibited by those cephalopods by the use of several families, have not been very successful. Kobayashi (1933, 1935a) divided these cephalopods into the Plectronoceratidae and Ellesmeroceratidae, apparently mainly on the basis of characters of the siphuncle. He regarded the Plectronoceratidae as varying from orthochoanitic to cyrtochoanitic (Kobayashi, 1933) and the Ellesmeroceratidae as grading from orthochoanitic to holochoanitic (Kobayashi, 1935a). The sections upon which the cyrtochoanitic condition is based are unfortunately rather faint,but the conclusion may be tentatively accepted until better evidence is at hand. Flower (1941a), found *Ellesmeroceras* to be aneuchoanitic and not holochoanitic, as Kobayashi believed, a condition which has subsequently been substantiated by unpublished thin sections.

Ulrich, Foerste and Miller (1943) and Ulrich, Foerste, Miller and Unklesbay (1944) divided these ellesmeroceroids into several families on the basis of an exceedingly artificial classification. Orthoceracones were placed in the ill-advised Orthocerotidae, endogastric cyrtoceracones in the Cyrtendoceratidae and straight brevicones in the Cyclostomiceratidae. Flower (1946) pointed out that the cephalopods of the Lower Canadian formed a closely knit group, and the genera distributed among these three families had much more in common, and less in common with other genera placed in those same families, than this current classifi-

cation would indicate. *Cyrtendoceras* is described as a holochoanitic endoceroid. If so, these endogastric Wanwanian cyrtoceracones should not be placed with it, for they have neither holochoanitic siphuncle walls nor endocones. The family, as thus employed, has no genetic significance. A much closer approach to a taxonomic expression of relationship can be attained by employing the Plectronoceratidae for the endogastric cyrtoceracones and the Ellesmeroceratidae for the orthoceracones of this group. Even so, difficulties are encountered, for there is no clear boundary between these two families. *Eremoceras* and *Ectenoceras* lie essentially upon the tenuous boundary between the orthoceraconic and cyrtoceraconic, and could be placed in either family with about equal justification. For these reasons it seems wisest in the present state of our knowledge to discuss the two families together.

Actual evidence as to the structure of the siphuncles in these forms is very meagre. Kobayashi (1933) published excellent sections of the Manchurian *Multicameroceras*, *Sinoeremoceras*, and *Wanwanoceras*. Unfortunately the limestones showed only rather faint color variation and the photographs were strongly retouched for illustration. Under such circumstances, interpretation of the original structure is extremely difficult. A connecting ring projecting within the siphuncle wall, after the manner of those of *Eothinoceras*, might present a very similar effect without being properly cyrtochoanitic. Unfortunately, it seems necessary to regard with doubt the adoral expanded connecting ring which Kobayashi (1935a) figured for *Plectronoceras*. Ulrich, Foerste, Miller and Unklesbay (1944) suggest that the structure figured may be adventitious and that *Plectronoceras* may have lacked connecting rings. The absence of connecting rings is a conclusion which we are reluctant to accept in view of their universal and very strong development in Lower Canadian cephalopods, but certainly is supported by the present evidence.

The siphuncle wall of *Ellesmeroceras* was figured by the writer (Flower 1941a). The septal necks are very short and are supplemented by thick connecting rings. Possibly some structural differentiation may have taken place within the ring, but the sections studied so far suggest such variation without being clear enough to demonstrate it conclusively. Subsequent thin sections of other species of *Ellesmeroceras* show similar septal necks, but fail to show the original state of the connecting ring clearly. Ulrich, Foerste and Miller (1943, p. 92), have illustrated a very clear section of a *Clarkeoceras*, showing a relatively long septal neck and a thick connecting ring. Except that no zonal differentiation in the ring is indicated, this section is very similar to that of our *Cyptendoceras* shown in Fig. 1c.

The evidence as to the structure of the siphuncle wall in these cephalopods is quantitatively meagre, but indicates aneuchoanitic to rather long ellipochoanitic necks, supplemented by rather thick connecting rings.

Within the siphuncles of some of these cephalopods diaphragms have been reported. The actual evidence of diaphragms is, however, again very meagre. The structures which Kobayashi (1933) figured as pseudodiaphragms in the Plectronoceratidae are so faint that they may well be inorganic. In America, the evidence for diaphragms crossing the siphuncle rests upon a mere handful of specimens. The structure is shown by one specimen of *Stemtonoceras elongatum*, two of *Levisoceras*, sp., and several of *Robsonoceras robsonense*. My own material has so far yielded clear diaphragms only in an undescribed species of *Dakeoceras*. Hyatt (1900) first reported these structures in *Diphragmoceras*, but the type species has never been figured, and only inadequately described. Clarke described diaphragms in *Clarkeoceras newton-winchelli* but Ulrich, Foerste, Miller and Unklesbay reported that the evidence for these structures is inconclusive.

A number of chert internal molds by which much of the American material of Gasconade age is represented, show siphuncle fillings which terminate rather abruptly in bluntly rounded tips. This may signify that infiltration of the matrix

into the siphuncle from the living chamber was stopped adapically by a diaphragm, the remainder of the siphuncle being filled only with inorganic calcite and later lost by solution along with the original shell parts. This interpretation is, of course, hypothetical. However, the postulation of diaphragms as an explanation of this phenomenon presents a logical answer to the problem set by these bluntly rounded siphuncle fillings. An organic rather than an inorganic cause is suggested by the occurrence of such abruptly terminated fillings in a group of cephalopods which form both a taxonomic and a stratigraphic unit, the ellesmeroids of the Lower Canadian. Such siphuncles have been illustrated for *Levisoceras*, *Oneotoceras*, *Caseoceras* and the Middle Canadian *Cumberloceras*, and are suggested, though less conclusively, in still other genera.

Admittedly, the meagre data at present do not supply a good basis for understanding the role of diaphragms in growth or function. Good evidence of the structures is so rare that it is uncertain whether they occur only in isolated individuals, whether they developed in only a few species, or whether they may be characteristic of genera which might even be set apart in a family by themselves. Actinosiphonate structure long presented the same problem, and the material by which it could be studied and evaluated was much more abundant than that showing diaphragms.

The limestones in America which yield ellesmeroceroids have not been widely studied faunally. Faunas under investigation by the writer promise to yield much information on the siphuncles of a number of the genera, but in their study the same difficulties are encountered as in the Wanwankou limestone of Manchuria and Korea; color differentiation is faint and makes it difficult to distinguish organic from inorganic features. The ellesmeroceroids clearly fail to show holochoanitic structure, and possess instead short necks and rather dense thick connecting rings. Diaphragms occur in the group, but are rare and of uncertain significance.

The genera which constitute the ellesmeroceroids have been summarized by the writer (Flower, 1946, p. 75–78). They include the Cambrian *Plectronoceras*, the Lower Canadian genera *Shelbyoceras*, *Dakeoceras*, *Burenoceras*, *Buehleroceras*, *Oneotoceras*, *Levisoceras*, *Caseoceras*, *Conocerina*, *Eremoceras*, *Ectenoceras*, *Ellesmeroceras*, *Walcottoceras*, *Robsonoceras*, *Endocycloceras* and *Albertoceras*. *Cumberloceras* and *Smithvilloceras* represent survivals of the stock in Middle and Upper Canadian, and *Cyrtocerina* and probably *Shideleroceras* represent the last survivors of the group persisting to the Richmond. Separate families have been erected for *Buttsoceras*, *Cyrtocerina* and *Shideleroceras*. The proper placing of the remainder in the *Plectronoceratidae* and *Ellesmeroceratidae* must await further study of the structure of the genera.

PROTEROCAMEROCERATIDAE

The family Proterocameroceratidae (Flower, 1946, p. 80), was erected for slender endoceroids with ellipochoanitic siphuncle walls. These are the oldest of the endoceroids and the most primitive. Their slender form sets them apart from the piloceroids, a few of which are also ellipochoanitic. The holochoanitic siphuncle wall distinguishes the Piloceratidae proper as well as the slender Endoceratidae. From the Ellesmeroceratidae the Proterocameroceratidae differ in two respects, the presence of endocones and the differentiation of parts of the connecting ring. The last difference may not be real, but only apparent, for as yet very few ellesmeroceroids have been studied from specimens well enough preserved to show this differentiation should it occur. *Ellesmeroceras bridgei* shows some indication of such specialization in the connecting ring, but the evidence is not conclusive.

Determination of the exact scope of the Proterocameroceratidae requires more information than is now available. Previously it has been assumed that all endoceroids were holochoanitic, and no detailed examination of the siphuncle wall was

undertaken. The discovery of aneuchoanitic necks and thick rings simulating necks in opaque section in *Proetrocameroceras*, (Flower, 1941), showed that a careful restudy of endoceroid siphuncle walls would have to be undertaken, preferably by the use of thin sections. Unfortunately this is made difficult by the rarity of suitably preserved material among the older endoceroids. Quite probably the Proterocameroceratidae contain all of the slender endoceroids older than the Chazyan. Certainly all of the Canadian slender endoceroids thus far studied from satisfactory material have yielded ellipochoanitic siphuncles. The number of species and genera which supply this evidence do not, it is true, make a very imposing assemblage. However, the scant evidence is unanimous in indicating ellipochoanitic structure in Canadian endoceroids. The genera in which such structure has been found include *Proterocameroceras*, *Clitendoceras* and *Cyptendoceras*. Suitable material for *Cotteroceras*, *Cyptendocerina*, *Paraendoceras* and *Mcqueenoceras* is not yet available; the extant material of these genera consists of shells which are either chert steinkerns or are extensively dolomitized so that the siphuncle wall is greatly altered. There remain generalized species which have been assigned to *Endoceras*. Sections made from such species indicate that they also are ellipochoanitic and are therefore not properly assignable to *Endoceras* or to the Endoceratidae.

The endoceroids of the pre-Chazyan have been distributed among various genera on the basis of cross section, suture pattern and form. *Proterocameroceras* was shown to be ellipochoanitic (Flower, 1941) and was therefore removed to the Orthocerotidae (Ulrich, Foerste, Miller and Unklesbay, 1944). No species other than the genotype was recognized. Other endoceroids were referred to the Endoceratidae. Straight compressed shells were assigned to *Cotteroceras*. *Clitendoceras* was used for shells which are circular, but have oblique sutures, sloping orad on the dorsum. Perhaps not enough stress was placed on the faint exogastric curvature shown by the genotype. *Cyptendoceras* was employed for depressed shells in which the sutures form ventral and sometimes dorsal lobes. *Cyptendocerina* also has ventral lobes, but the siphuncle is farther from the venter. *Mcqueenoceras* is faintly endogastric, and closely allied to *Clitendoceras*. *Pachendoceras* is employed for depressed shells with a flattened venter and transverse sutures. *Paraendoceras* is distinctive in its rather rapid expansion, approaching some of the more slender shells which have been grouped by Kobayashi with the piloceroids. The more generalized of the species assigned to *Clitendoceras* and *Cyptendoceras* approach very closely to those Canadian shells which have been placed, we think mistakenly, in *Endoceras*. A survey of the Canadian species placed in *Endoceras* shows that not one exhibits evidence of a holochoanitic siphuncle, and many lack evidence of endocones. Many are not true endoceroids, and none are demonstrably members of the Endoceratidae.

It is within the Canadian Proterocameroceratidae that evidence exists of the specialization of the connecting ring and of modifications of the septal neck approaching, but not attaining, a holochoanitic condition.

DEVELOPMENT OF THE SEPTAL NECKS

As previously shown, the meagre evidence indicates that in the ancestral Ellesmeroceratidae the septal necks vary in length, but none have been found which are long enough to be called holochoanitic. The shells which are most similar to the true endoceroids are those of the genus *Ellesmeroceras*, which, indeed, is most readily differentiated from the endoceroid by the absence of endocones. Happily, the actual morphological data is largest for this crucial genus, and indicates uniformly necks so short as to be properly aneuchoanitic. (Fig. 1A).

Within the Proterocameroceratidea, *Proterocameroceras* itself possesses aneuchoanitic necks similar to those of *Ellesemroceras* and *Eurystomites* (Flower, 1941), (Fig. 1B). *"Cameroceras" annuliferum* Flower, a species which is probably best

placed in the genus *Cyptendoceras*, although it is admittedly generalized in respect to section and sutures, shows short orthochoanitic necks supplemented by connecting rings. *Clitendoceras* has been observed to show a gradual adoral lengthening of the necks in a series of camerae. An undescribed Middle Canadian *Cyptendoceras* (Fig. 1C) shows septal necks which are essentially funnel-shaped rather than tubular. These extend far enough apicad to be at a level with the bend of the next adapical septum, but are so far removed from the septum that the condition escapes being properly holochoanitic. The septal necks of *Coreanoceras* (Kobayashi, 1935) are only slightly longer ventrally. It is perhaps significant that in this genus the condition approaches the holochoanitic without quite attaining it. Further, these same shells, though grouped as piloceroids by Kobayashi, have only moderately expanding siphuncles and phragmocones. In both respects they are intermediate between the Proterocameroceratidae and the Piloceratidae.

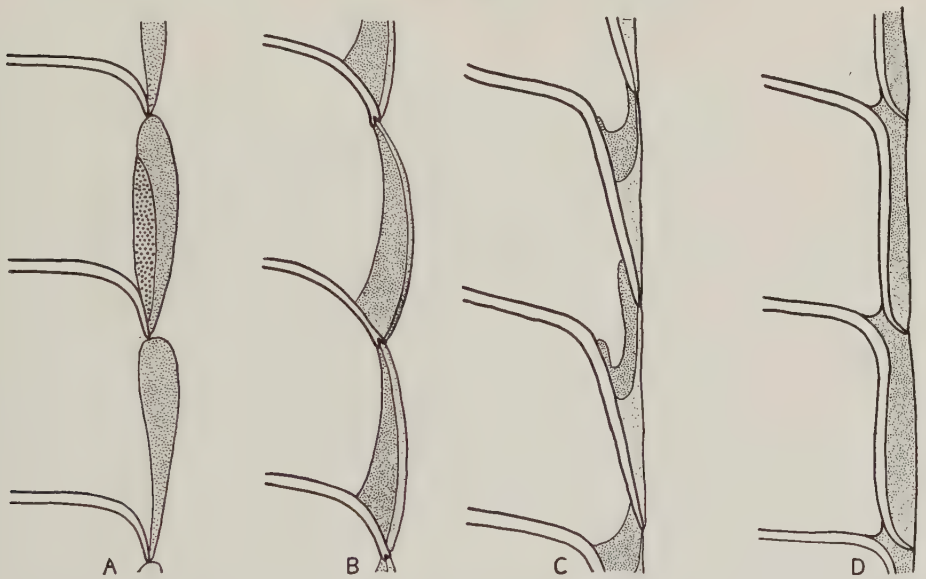

FIG. 1. Stages in development of holochoanitic spihuncle wall. A. *Ellesmeroceras*. Aneuchoanitic necks and thick rings. The middle ring shows differentiation of an outer layer suggested by *Ellesmeroceras bridgei* Flower. B. Double layer of connecting ring, as developed in *Proterocameroceras;* based on *P. brainerdi*. C. Intermediate stage, showing incipient concentration of central layer at apex, from *Cyptendoceras*. D. Development of holochoanitic necks, with concentration of dense material making up central layer in B and C at apex, forming eyelet. From *Vaginoceras oppletum* Ruedemann.

THE CONNECTING RING

The progressive series already traced on the basis of the septal neck is supported by stratigraphic evidence, but in itself would be weak without the corroborative evidence supplied by the connecting ring. The ellesmeroceroid-endoceroid line is characterized by connecting rings which are generally and perhaps uniformly thicker than those of the line containing most ellipochoanitic cephalopods. Further, connecting rings of this type show generally some sort of structural differentiation. Two distinct and seemingly diametrically opposed types of structure were found, one in which the connecting ring was divided into an inner and an outer zone, the inner (central) zone consisting of denser and finer grained material than the outer zone. In contrast, a second type was found in which the denser and finer material was concentrated at the tip of the connecting ring. The banded

types (Fig. 1B), were first noted in *Proterocameroceras* and in *Eurystomites*, the other type (Fig. 1D), to which I gave the name of eyelet, was found in *Tarphyceras* and in *Endoceras* and *Vaginoceras*. Subsequently it was found in *Cassinoceras*, and there is reason to believe that it is present in *Piloceras* also.

No great taxonomic significance could be given to these diametrically opposed types of connecting rings, for it was obviously unthinkable to unite *Tarphyceras* closely with true *Endoceratidae*, and to unite *Eurystomites* with the endoceroid genus *Proterocameroceras*. To do so would necessitate passing over the strong evidence supplied by section and ontogeny connecting *Eurystomites* and *Tarphyceras* (Hyatt, 1894) and also the evidence supplied by not only form similarity but also the structural patterns of the endosiphuncles of *Proterocameroceras* and the Endoceratidae. Obviously these two types of structure represent variations of a single fundamental structural pattern under the influence of secondary factors which worked indepednently in the Tarphyceratidae and Endoceroidea. Inspection of the nature of the materials of the connecting ring suggests that the central or innermost layer of the zonal pattern is the homologue of the eyelet in the end ceroid pattern. Both consist of dense fine grained to amorphous material, while in contrast the remainder of the connecting ring is crystaline or coarsely granular. Further, the two structures behave very differently under various conditions of preservation. Examples are known of preservation of the eyelet and the inner zone while the remainder of the ring is incomplete or altogether destroyed. When the two types of structure are viewed in relation to the septal necks some suggestion of a solution is found, for the zonal condition is found thus far only in cephalopods with aneuchoanitic necks, but where the septal necks are long, in the connecting ring, which invariably extends from the tip of one neck apicad to the tip of the next, the portion lying within the adapical neck has developed into the eyelet. This is true of *Tarphyceras*. It was not as obvious for *Endoceras*, for the entire length of the connecting ring lies within the next adapical septal neck. Why was not the entire length of the ring given over to structure of the eyelet type? An explanation is suggested by the nature of the materials concerned. If the endoceroids, as was certainly true of many other cephalopods, maintained a connection throughout life between tissues lining the camerae and those occupying the siphuncle, such a connection could have taken place only through a permeable connecting ring. The typical connecting ring was therefore assumed to be secreted within tissue (Flower, 1939), and to maintain a porous character throughout life. As a structure through which such materials must have passed, the ring must remain porous. The eyelet, however, is clearly a part of the ring which is made of dense fine grained amorphous material, which could hardly have been porous. Therefore, it is natural that such material should concentrate in that part of the connecting ring which lay within the next adapical septal neck, where, because of the solid nature of the neck opposing it externally, no metabolic connection existed. Such differentiation of materials may or may not have been completed prior to the perfection of the holochoanitic siphuncle of the Piloceratidae. However, if a metabolic connection between camerae and siphuncle was maintained in holochoanitic shells prior of course to the filling in of the adjacent part of the siphuncle by endocones, such a connection must have taken place through the adoral part of the connecting ring, passing between the septa.

How any such connection was maintained in aneuchoanitic shells with a zonal arrangement of the materials of the connecting ring is uncertain. Either no connection could have existed, or else the inner zone was more porous than was the eyelet. The nature of the material as seen in sections suggests the second explanation, but I do not consider the evidence conclusive. There is no evidence to suggest that the camerae were sealed from the remainder of the shell by delayed secretion of the inner zone; on the contrary, the inner and outer zones were either secreted together, or else the outer zone appeared after the inner one; certainly not

before. There is some indication that the outer zone may have thickened by subsequent growth, as suggested by laminae shown in the clearest of the sections. Certainly cameral tissue is a primitive, rather than a specialized, feature and one therefore presumably present in these older cephalopods. The fact that evidence of cameral deposits is nonexistent in the ellesmeroceroids and requires further study in endoceroids before its presence can be conclusively accepted is beside the point.

The faint suggestion of zonal arrangement in *Ellesmeroceras bridgei* Flower (1941a), as indicated in one segment of Fig. 1A, is not conclusive. However, it does suggest that the zonal arrangement is primitive and the eyelet structure developed from it, for the ellesmeroceroids are clearly both older and more primitive than those cephalopods known to show the eyelet.

New material, in the form of a section of an undescribed species of *Cyptendoceras* supplies evidence which forms some basis for this reasoning. The section (Fig. 1C), is intermediate in both the length of the septal neck and the arrangement of the dense material of the connecting ring, between the condition found in *Proterocameroceras* on one hand and that found in *Endoceras* on the other. The septal necks, as already noted, are nearly holochoanitic, but are widely separated because their pattern is conical rather than tubular. The intervening connecting ring is of such a nature that it can be interpreted in terms of either the zonal or the eyelet pattern being an intermediate phase connecting the two. An inner and outer zone can be clearly recognized, but the inner zone is greatly thickened adapically. Likewise, one can interpret the same section as an eyelet which is stretched orad along the inside of the main part of the ring, while the main part of the ring is thickened and somewhat folded around the bend of the septum at its adapical end.

Clear development of the eyelet pattern in an ellipochoanitic endoceroid has not been found. *Cyptendoceras annuliferum* (Flower) showed traces of the eyelet in relatively thick transparent sections. The clarity of the eylet was lost in reduction of the thickness of the section for photography. It is a curious fact that both the eyelet and the perispatial deposits of actinoceroids may be reduced to a point at which they become nearly invisible in the thinnest of sections. Unfortunately they are best displayed in sections thick enough that the contrast between calcite-replaced shell parts and the matrix are so strong that they are not suitable for photography. *C. annuliferum* displays eyelets which are essentially similar to those found in *Tarphyceras seelyi* (Flower, 1941, Pl. 1, Fig. 2, Pl. 1, Fig. 9–10).

While much more remains to be learned about the nature, function and possibilities of radial variation in clarity and distribution of the eyelet in endoceroids, the main point of the structure is that it demonstrated clearly that the connecting ring is retained in the holochoanitic Endoceroidea. This is indicated not only by the phyletic sequence postulated in Figs. 1B-D, but also by the identity of the structure of the connecting ring in *Nanno* and *Vaginoceras* with that of *Centrotarphyceras* (Flower, 1941). Prior to this, the existence of the connecting ring in holochoanitic cephalopods was not recognized. Hyatt (1900) presented a figure of *Endoceras proteiforme* (Fig. 2) showing holochoanitic necks separated by bands which are apparently morphologically distinct from them. The tip of the neck and the tip of this unidentified band are separated by areas indicated in black, which correspond to the eyelet. Hyatt never amplified the complexities of structure indicated in this diagram and his interpretation of these structures is therefore somewhat dubious. However, he never mentioned the presence of a connecting ring. Ruedemann (1906, Fig. 3, p. 413) reproduced Hyatt's figure, and showed a similar structure in *Vaginoceras oppletum* (Pl. 4, Fig. 2–3). This specimen fails to show clearly the differentiation between the septal neck and the connecting ring which arises from its tip. Without this differentiation, the structure seems to be that which Hyatt (1900) had earlier attributed to the genus

Vaginoceras. As a consequence, it is not unnatural that Ruedemann interpreted it as such, and on the basis of this structure assigned his species to the genus *Vaginoceras*. Of the dense and darker colored areas which represent the eyelets Ruedemann says: "The structure of the siphuncular wall, which is here that of a *Vaginoceras*, would suggest that the pseudosepta extend through or caused the collarlike interspace which enters between the septum where it bends into the septal neck and the septal neck of the next younger septum which at this point bends slightly outward." The structures are extremely confusing, and it was not until the species had been examined by abundant thin sections, each of which indicated the same structural pattern, that it became clear that the morphological interpretation must be revised.

The presence of a connecting ring in the holochoanitic Endoceratidae indicates a conclusion already voiced by Kobayashi on the basis of endosiphuncular structures, that the endoceroid was not primitive but highly specialized. Further, it

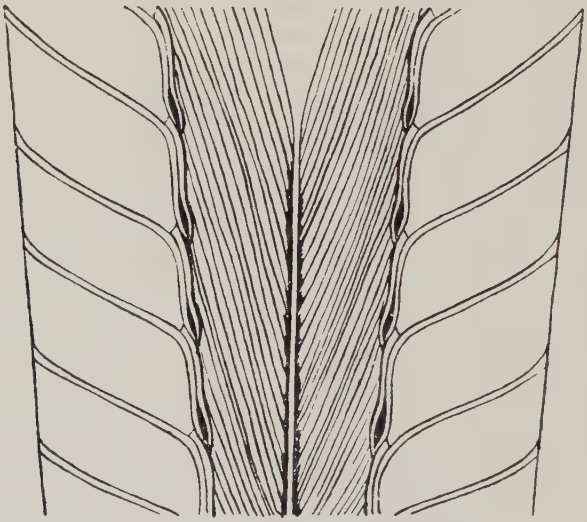

FIG. 2. Section of *Endoceras proteiforme* Hall, after Hyatt. The septal necks are shown as holochoanitic, but supplemented by other unidentified structures which correspond to the main part of the connecting ring. The adapical tips of the rings are shown as separated from the necks by black areas. These represent the eyelets, properly a part of the rings, as shown by thin sections. Within is shown the endosiphuncle, with numerous endocones terminating in an endosiphotube.

indicated that the endoceroid must have had an ancestry which was ellipochoanitic. Later investigations revealed that this ancestral phase was much more widespread than Kobayashi had realized, for it embraced not only the Plectronoceratidae, which he had shown to have short necks supplemented by connecting rings, but also the Ellesmeroceratidae and the older of the shells which had previously been assigned to the Endoceratidae. This required more a revision of a conception of morphology than one of relationship for, while it was an error to consider the Ellesmeroceratidae and the older Endoceratidae as holochoanitic, the fact remained that the structure of their siphuncle walls was practically identical, and in both groups the thick connecting ring did not simulate a septal neck very closely except in the most favorably preserved material.

Material suitable for a proper study of zonation in the connecting ring of *Ellesemroceras* has not yet been found. *Ellesmeroceras expansum* Flower (1941A, Fig. 1A-B, Pl. 1, Fig. 9, Pl. 2, Fig. 6), shows evidence of some dark material which

lies in a few of the camerae between the white calcite which has replaced the connecting ring and the white calcite which forms a chemically deposited filling for some of the camerae. This suggests the possibility of a banding of the connecting ring such as is indicated in text Fig. 1A in the upper complete segment. The transverse longitudinal section of the same species (Flower, 1941A, Pl. 1, Fig. 10), also shows a suggestion of such zonation. However, other parts of the phragmocone lack evidence of these structures and further information is needed. Material of *Ellesmeroceras* from eastern New York has thus far been found to be too extensively recrystallized to yield much additional information.

Where banding is well developed it forms a pattern in which the inner zone is fairly uniform in thickness throughout its length, while the outer zone is widest adapically. This structural pattern is fairly widespread among Canadian nautiloids, and is not by any means confined to the Proterocameroceratidae. It was figured by the writer for *Proterocameroceras* and *Eurystomites*. Ulrich, Foerste and Miller (1943), p. 56, Fig. 3B), have shown the same structural pattern in *Cyclostomiceras cassinense*. Subsequently the same structural pattern has been observed in my own material of *Onychoceras* and *Bassleroceras*. Among orthoconic types it is present in *Baltoceras*, and *Protocycloceras* shows a siphuncle wall which is probably a slight modification of this pattern. Ulrich, Foerste, Miller and Furnish have figured several siphuncles of Canadian nautilicones which appear to have this structure. *Aphetoceras attenuatum*, shown on their Pl. 25, Fig. 6, is very close to *Eurystomites*, although the resemblance is much less marked in the drawing (text Fig. 3, p. 19) of the same section. *Campbelloceras rotundum* (Fig. 10, p. 47, Pl. 50, Fig. 5) shows a suggestion of zonal development, though the irregularity of the structures is again accentuated in the drawing. Here the connecting ring in the ventral siphuncle is so thickened ventrally as to nearly fill the space between the cavity of the siphuncle and the ventral wall of the shell. Such sections suggest that the connecting ring grew after it first appeared by the addition of material to its cameral surface. Whether such deposits of the connecting ring grew outward into the camerae in *Curtoceras* is still uncertain, but such a possibility is strongly suggested by Ulrich, Foerste, Miller and Furnish (Pl. 50, Fig. 3).

Cyptendoceras sp. (Fig. 1C) is thus far the only specimen showing a combination of transitory phases of the septal neck between ellipochoanitic and holochoanitic with a transitory phase between the eyelet pattern and the presumably more generalized zonal condition. Similar conditions are to be expected in some of the Asiatic piloceroids, in particular *Kotoceras*, but the only figure of the siphuncle wall available (Kobayashi, 1936, Pl. 22, Fig. 13), is not enlarged sufficiently to show this. Further, in this specimen, which is an opaque section, differentiation of the septal neck and the connecting ring is not clear.

PILOCERATIDAE

Flower (1941) reported in *Cassinoceras explanator* (Whitfield) structures within the siphuncle which seemed to represent connecting rings, complete with the eyelet, which suggested that the siphuncle was holochoanitic and had essentially the structure observed more fully by means of thin sections in *Vaginoceras oppletum* Ruedemann. Later sections have served to confirm this view. Ulrich, Foerste and Miller (1943) p. 22, found similar structures in *Piloceras invaginatum* Salter, but did not recognize them as connecting rings. They describe them as follows: "The inner surface of the septal necks is lined by a black layer which is about 0.4 mm. thick and which terminates as a thin edge at the adapical end of each neck. The adoral portion of this black layer extends between the adoral end of a septal neck and the adapical end of an adjacent neck for a distance of about 1 mm. along the adoral surface of the septum which gives rise to the adapical neck. Along the inner surface of the siphuncle there is a discontinuous series of these black layers each one 'pinching out' at the adapical end of the septal neck which it lines."

This might almost be a description of the connecting ring shown in Fig. 1D, and there can be little doubt but that it represents an identical structure except that there is no mention of the eyelet. Indication of the eyelet is very plain in *Cassinoceras explanator*.

Happily, the presence of connecting rings within the septal necks in these two species, which are the genotypes of *Piloceras* and *Cassinoceras*, show that the Piloceratidae proper are holochoanitic.

The origin of the Piloceratidae is clearly to be sought in the Proterocameroceratidae itself. Perhaps some of the lesser known slender shells which have been considered piloceroids in Asia may supply the link. *Coreanoceras*, the only member of this group of shells for which the siphuncle wall is known, is ellipochoanitic, as shown by Kobayashi (1935a). This shell is so slender, however, that it seems it might be grouped as easily with the *Proterocameroceratidae* as with the piloceroids; certainly it differs markedly in aspect from the broadly expanded siphuncle of *Chilihoceras*, with which Kobayashi would group it.

It should be pointed out also that we have no evidence as to the position of *Chilihoceras* Grabau, *Manchuroceras* or the closely allied and probably synonymous *Liaotungoceras* Shimizu and Obata in this scheme. The endosiphunclar specializations of *Chilihoceras* described by Grabau are so remarkable that other students of cephalopods, who have, it is true, not seen the material, are a bit reluctant to accept the rather complex interpretation of the endosiphuncle which Grabau presents. *Manchuroceras* and *Liaotungoceras* were depressed siphuncles. In true Piloceratidae, in which I should include *Piloceras*, *Cassinoceras* and *Allopiloceras*, both the conch and the siphuncle are compressed. The endosiphuncular differences together with the differences in form suggest that the depressed Asiatic genera have undergone a development independent of that of the Piloceratidae, and the two lines may have separated prior to the development of holochoanitic necks. Kobayashi (1935, p. 750), idicates ellipochoanitic necks for the Chiloceratidae, but to the writer it seems unwise to unite the strongly breviconic *Chilihoceras* with the smaller and much more slender *Coreanoceras*, which supplies the only basis for making any statement concerning the siphuncle wall.

ENDOCERATIDAE

While the origin of the Piloceratidae is somewhat obscured by lack of information concerning the structure of possibly crucial genera of Asiatic piloceroids which may supply connecting links with the Proterocameroceratidae, there is enough evidence to show that between these two families occurred the transition from the ellipochoanitic to the holochoanitic siphuncle. The descendants of the piloceroids are easier to trace.

With very few exceptions, it has been seen that the Lower Canadian, with which the Gasconade and Wanwanian are synonymous, contains the acme of the ellesmeroceroids. The Middle Canadian however, shows a maximum development of the Proterocameroceratidae. The Upper Canadian is marked by the piloceroids. The Longview limestone of Alabama furnishes one of the few exceptions. This supposedly Middle Canadian formation contains *Cumberloceras*, which is morphologically a Lower Canadian type, and also *Allopiloceras*, elsewhere confined to the Upper Canadian. Other members of its fauna are essentially Middle Canadian. I have observed similar phenomena, involving a mingling of Lower and Middle Canadian types locally in the Fort Ann region of eastern New York, but closer study has shown that due to deposition of Middle Canadian beds on an uneven erosion surface, in some places fossiliferous Lower and Middle Canadian limestones very similar lithologically, are brought into juxtaposition. So anomalous is the fauna of the Longview that it might be re-examined with this possibility in mind. At present, I am reluctant to accept it as evidence of the appearance of piloceroids in the Middle Canadian.

At the close of the Canadian the Piloceratidae disappear. The Proterocamerocertidae, which dominate the Middle Canadian, persist into the Upper, and become highly specialized, as shown by the siphuncle of *Proterocameroceras* itself. Even more bizarre specializations are found in *Meniscoceras*, the only known survivor of the Proterocameroceratidae in the Chazyan.

The Chazyan marks the appearance of a new stock, the Endoceratidae. This family contains longiconic shells, among which are to be found the largest of our straight cephalopods. They differ from the Proterocameroceratidae and agree with the Piloceratidae in possessing holochoanitic septal necks with the connecting rings within (Fig. 1D). This structural agreement suggests that perhaps the Endoceratidae may have descended from the Piloceratidae rather than from the Proterocameroceratidae which they resemble more superficially. Examination of the morphological facts with this possibility in mind yields some corroborative evidence. The true piloceroids are compressed. Although Endoceratidae are dominantly depressed in section in the adult, the early stages are dominantly, if not uniformly, compressed. Further, among the first of the true Endoceratidae are found those peculiar early stages which have long gone under the generic name *Nanno*. Schindewolf suggested that *Nanno* represented a retention of a preseptal phase, harkening back beyond the point in evolution at which the shell could even be classed as a cephalopod, close to the archetypical mollusc. Yet strangely enough nothing similar to *Nanno* appears in the earlier sediments. *Nanno* ranges from Chazyan to Richmond. The only earlier cephalopod which suggests it at all is the little known *Mysticoceras* of Canadian age. Certainly *Nanno* puts in too late an appearance to be interpreted according to Schindewolf's suggestion. Instead, its stratigraphic position suggests that it may represent the recapitulation of a *Piloceras* stage in the development of the Endoceratidae.

Among undisputed Ellesmeroceratidae no apical ends of the siphuncles are known. Enough specimens approach close to the apex to suggest that the siphuncle was small and marginal from its very beginning. *Pachendoceras*, as noted above, may be an ellesmeroceroid instead of an endoceroid. One specimen (Ulrich, Foerste, Miller and Unklesbay 1944, Pl. 61, Fig. 4), was interpreted as a specimen bearing an annulated endocone. This interpretation is based upon the fact that the apically protruding siphuncle bears annuli which are more widely spaced than are those indicated farther orad by the preserved camerae, or, for that matter, by the adoral part of the siphuncle which extends orad of the camerae. The interpretation of this specimen as an apical end rests upon (1) its small size in relation to other representatives of the species and (2) the fact that septation commonly varies in the early stages of primitive endoceroids, and the difference in spacing of the septa does therefore, not necessarily indicate the conclusion drawn from this specimen by its describers.

In the Proterocameroceratidae a very similar apical end of a siphuncle was described by the writer (Flower, 1941) as *"Cameroceras" annuliferum* (Fig. 3D). The nature of the siphuncle wall proclaims this form a member of the Proterocameroceratidae. Subsequently collected material from the type locality indicates that the species is rather generalized in form, but is close to some of the more generalized species which have been assigned to *Cyptendoceras*. Further, a similar small siphuncle has been found in the early stages of an unquestionable *Cyptendoceras* from the Fort Ann region. Both specimens show a siphuncle which contracts slowly toward its tip, and in both there is the faintest suggestion of a very tiny apical bulbous inflation. These facts are significant to the present discussion mainly in indicating that in the Lower and Middle Canadian Ellesmeroceratidae and Proterocameroceratidae there is no indication of a siphuncle which expands rapidly and may even occupy the entire diameter of the apical part of the shell.

Apices of siphuncles are well known in the Piloceratidae, but are invariably free from the phragmocone. Here both the phargmocone and the siphuncle expand

very rapidly. Although the camerate region of the shell is very tiny in the apical region, the evidence suggests that in all three of the genera the phragmocone extends very close to the apex, if not completely to it. (Fig. 3A.)

The next stage in development is marked by a tendency for the adoral part of the siphuncle to become slender. Sometimes the siphuncle assumes a more slender form gradually, but in a few species the transition is abrupt. Further, in these same species there is only poor and inconclusive evidence of septation on the outside of the siphuncle; such faint annuli as exist may be septa; on the other hand similar markings would be expected as relics of septa in shells in which the siphuncle has expanded so as to crowd out the camerae completely. Although such a conclusion is somewhat venturesome, I have indicated it in my interpretation of

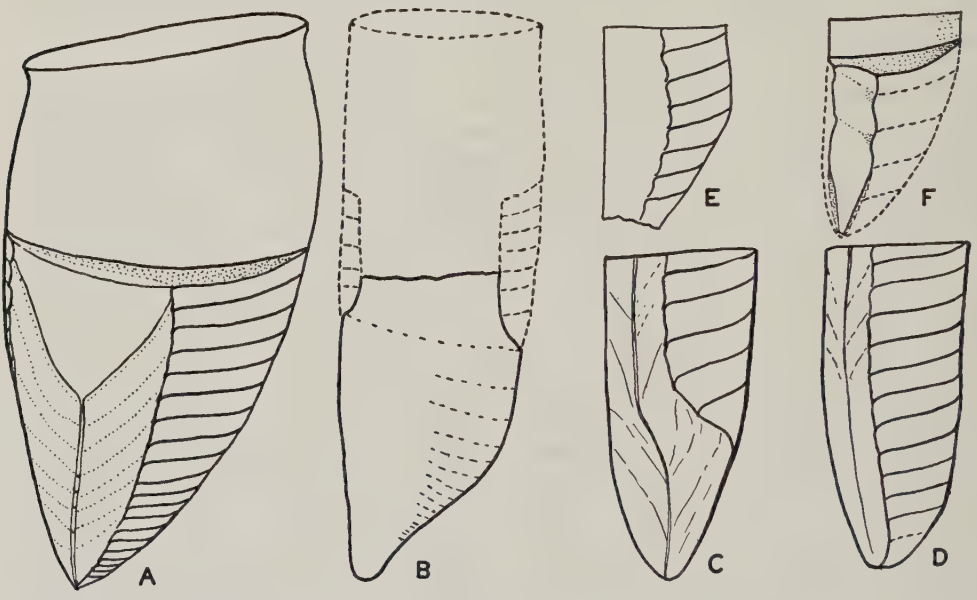

FIG. 3. Apical condition of siphuncles in endoceroids. A. *Cassinoceras*, with entire phragmocone expanding rapidly, but marked acceleration in expansion of siphuncle beyond that of the conch. B. *Allopiloceras*, based upon the specimen of *A. sevierense* showing the most marked adoral contraction of the siphuncle. Phragmocone and living chamber reconstructed. C. Vertical section through *Nanno*, based upon *N. noveboracum* Ruedemann. D. Apex of *Cyptendoceras annuliferum* (Flower). E. *Suecoceras*. F. Apex of *Endoceras*, based upon specimens currently assigned to *Cameroceras trentonense*. Shell restored over apex.

Allopiloceras (Fig. 3B), based upon a specimen of *A. sevierense* (Ulrich, Foerste and Miller, 1943, Pl. 3, Fig. 4), and have ventured to reconstruct a hypothetical phragmocone and living chamber for this species.

If such an apex is reduced in size, and the slender siphuncle indicated in this *Allopiloceras* is continued through a series of camerae in a slender phragmocone, a condition is developed which is essentially that of *Nanno noveboracum* Ruedemann (1906) of the Chazyan limestone (Fig. 3C). On this basis it is possible to explain *Nanno* as a recapitulation of a *Piloceras* stage, and the Piloceratidae-Endoceratidae sequence as a palingenetic one. *Nanno* persists into the Richmond, where a number of fine siphuncles, soon to be described, have been found. Some of these are startingly similar in proportions to those siphuncles which Holm (1896,) figured for *Nanno belemnitiforme* of the *Orthoceras* limestone of Sweden.

Continuation of the tachygenetic sequence would explain *Suecoceras* (Fig. 3E), as a slight reduction of the *Nanno* phase; the apex of the siphuncle is still swollen

and then contracted into a slender tube, but septation reaches the apex of the conch. Reduction of the swelling produces the apical ends which have been known as *Cameroceras* (Fig. 3F), and *Foerstella*. The genotype of *Foerstella* shows by the structure of the siphuncle wall that it is a true member of Endoceratidae. I have as yet had no material for sections of the type of *Cameroceras*, but there can be little doubt but that *Cameroceras trentonense* is nothing more than the apical stage of several species of *Endoceras* which occur as adult shells, though devoid of the apex, in the same beds. Among these forms is *Endoceras proteiforme*, the genotype.

Features of the endosiphuncle remain fairly uniform in the Endoceratidae, and differ from those of the Piloceratidae only in the simplification of the form of the endocones, which lack the wrinkling sometimes found in *Cassinoceras*. No important difference is to be found in the siphuncle walls between the two families. Yet the differences in shape are so great that the relationship was not previously suspected. However, it is now apparent that not only are there strong structural bonds uniting these two families, but that the slender endoceroids of the Canadian, which resemble the Endoceratidae superficially, differ from them widely in structure.

CONCLUSIONS

The morphological evidence yielded by thin sections of siphuncle walls shows that the holochoanitic type of structure is not dominant in a large group of cephalopods of which the endoceroids are a part, but instead is a specialization which is developed only in a small and highly specialized group of the Endoceratida, comprising the families Piloceratidae and Endoceratidae. The beginning of the stock is to be found in the oldest of our cephalopods, the ellesmeroceroids, which lack endocones, occasionally possess diaphraghms, but possess short septal necks supplemented by thick connecting rings. The Proterocameroceratidae, the first and simplest of the true endoceroids, differ from the ellesmeroceroids mainly in the addition of endocones to a shell which is otherwise essentially that of an ellesmeroceroid. Within the Proterocameroceratidae two trends are evident, first, the differentiation of parts of the connecting ring, producing either a zonal pattern or an eyelet. Happily connecting links are found showing that the two structural types are closely related. Second, in this family there is a tendency toward elongation of the septal necks. Necks long enough to be holochoanitic are found first in the Piloceratidae, accompanied by connecting rings, clearly a heritage from their ancestors of the Proterocameroceratidae. The rapid expansion of the piloceroid shell is necessarily coenogenetic. The Endoceratidae of the Ordovician are descended from the Piloceratidae with which they agree in the holochoanitic siphuncles retaining connecting rings. The rapid expansion of the siphuncle and the compressed condition of the piloceroid are recapitulated in the early stages of the Endoceratidae as shown by *Nanno*. Tachygenetic reduction of this stage produces more generalized early stages typified by *Cameroceras* and *Foerstella*. In gross features such apical ends resemble those of the Ellesmeroceratidae and Proterocameroceratidae, but differ from them in the holochoanitic septal necks.

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Reptiles and Amphibians of the Northeastern States

Ohio naturalists will be interested in obtaining the recently published booklet, Reptiles and Amphibians of the Northeastern States, written by Roger Conant, who is also the author of the standard reference, "Reptiles of Ohio." Formerly curator of reptiles at the Toledo Zoo and now curator of the Philadelphia Zoological Garden, Conant has written this 40-page non-technical resume as a publication of the Zoological Society of Philadelphia for the benefit of nature enthusiasts of that region. It deals with the snakes, lizards, turtles, frogs, toads, and salamanders of the northeastern states from Maine through New York, Pennsylvania and Maryland, and the coastal plain region of New Jersey and Delaware. Each of the 86 species listed is described briefly and is illustrated in a clear black-and-white photograph. Many of these photographs will suffice for identifying specimens. Photographs of juvenile snakes and turtles are given when such juveniles differ in pattern from their adults. In addition to the species' description, each group dealt with carries a short, well-written article on various phases of its biology. Also, there are directions for giving first aid in snake bite, and for the care of captive specimens. No taxonomic keys are included, but there is a useful reference list to more technical works. Although this booklet deals with the herpetological fauna from Pennsylvania eastward, it includes the majority of such species usually collected in Ohio, particularly in the eastern portion of the state. This booklet should find extensive use in the hands of high school biology students, scout organizations, and field naturalists throughout this entire region.—*John W. Price.*

Reptiles and Amphibians of the Northeastern States, by Roger Conant. Zoological Society of Philadelphia. 40 pp., 9x11¾ in. 1947. Price $1.00.

SPIROGYRA HOLLANDIA, A NEW SPECIES FROM NEW GUINEA

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The type material was collected at Hollandia, Dutch New Guinea, by Mr. Robert Sigafoos, now at the Harvard Biological Laboratories. Collections from Biak, Dutch New Guinea, made by Dr. M. E. Britton, Northwestern University, established the limits of variability of the species as it is now described.

The writer expresses his appreciation to Mr. Sigafoos and Dr. Britton for the material, and to Dr. E. N. Transeau, Professor Emeritus of this department, for his criticisms and for the use of his unpublished monograph on the Zygnemataceae which made possible the segregation of the species.

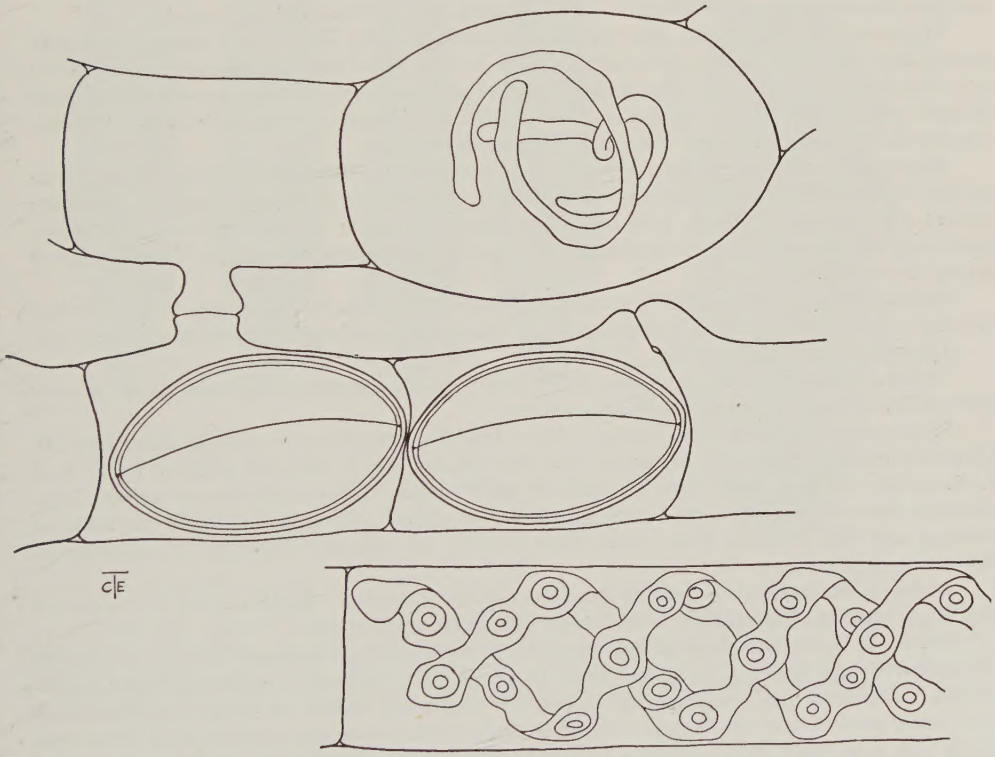

FIG. 1. *Spirogyra hollandia* sp. nov. Conjugating filaments showing lateral and scalariform conjugation, mature zygospores and a sterile cell. A portion of a vegetative cell is also shown.

Spirogyra hollandia sp. nov.

Vegetative cells 36–41μ x 60–192μ with plane end walls; 2 chromatophores, broad with large pyrenoids, making 1.5–2.5 turns in the cell; conjugation usually lateral, rarely scalariform; tubes formed by both gametangia; sterile cells sometimes inflated; receptive gametangia clyindric or enlarged; zygospore ellipsoid with rounded ends, 38–42μ x 62–78μ, median wall smooth, bright yellow at maturity.

Dutch New Guinea: Hollandia (Robert Sigafoos Coll.): Biak (M. E. Britton Coll.).

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[1]Paper from the Department of Botany, The Ohio State University, Columbus, Ohio. No. 498.

NEW BUPRESTIDAE WITH NOTES (COLEOPTERA)

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Acmaeodera fisheri vermiculata n. var.
(Fig. 7)

Male.—Size and form of *A. fisheri* Caz.; head and pronotum dark bronze, elytra yellow with dark brownish bronze maculations forming irregular lines; ventral surface obscured by white tomentum.

Head convex, surface densely, lightly punctured, obscured by long pubescence; antennae extending past middle of pronotum when laid along side, serrate from fifth segment.

Pronotum wider than long, widest back of middle, wider at base than at apex; side margin broadly rounded; anterior margin broadly lobed in middle; basal margin obliquely truncate from each side; disk convex, slight depression in middle at base; surface with densely placed large shallow punctures which are more numerous at sides, moderately clothed with long fine pubescence which is intermixed with white flocculent scales at edges.

Elytra at base not as wide as widest part of pronotum; sides expanded back of base, constricted in front of middle, expanded back of middle then broadly rounded to rounded, serrulate apices; disk convex, umbone prominent, depression at base; surface striately punctured, punctures less than their own diameters apart, interspaces minutely punctate, an upright hair arising from each.

Abdomen beneath finely, densely punctured, punctures hidden by tomentum, last abdominal segment very broadly rounded, lacking carina. Prosternum retracted, anterior margin straight.

Length 6 mm.; width 2.1 mm.

Female.—Somewhat stouter than male; last ventral abdominal segment more acutely rounded; outer antennal segments less transverse.

Holotype male labeled Palm Springs, Calif., June 30, 1946, allotype same locality, June 20. Paratypes from same locality and dates, also June 30 and July 9, 1941, all collected by D. J. & J. N. Knull; Phoenix, Ariz., May 24, 1936, R. H. Crandall. All in collection of writer. Also twenty miles east of Mesa, Ariz., June 11, 1942, Van Dyke[2] collection, California Academy of Sciences and Bill Williams Fork, Ariz., June 5, 1937, W. Benedict collector, in collection of University of Kansas.

At first I was inclined to consider this form a distinct species. Further study convinces me that it is a variety of *fisheri* Caz. which varies with immaculate elytra.

Dr. E. C. Van Dyke has kindly compared it with type of *A. vanduzeei* Van D. and states: "It is shorter and stubbier, *vanduzeei* being longer, 8 mm.; narrower and more attenuate posteriorly; anterior clypeal margin more widely, less angulately incised at middle; pronotum but little wider than elytra, moderately arcuate laterally while in *vanduzeei* considerably wider than elytra with sides much more evidently arcuate and pronotum in latter more coarsely, closely and deeply punctured; elytral markings of new species more or less opaque black and somewhat lineate in arrangement, while in other decidedly bluish, shining and more irregular in arrangement much as in *A. labyrinthica* Fall; punctate striae also more deeply impressed."

Dicerca strandtmanni n. sp.
(Figs. 5 and 6)

Female.—Resembling *D. divaricata* (Say) in color and form without prolonged apices of elytra.

Robust; color cupreous bronze throughout; pubescence inconspicuous above, longer beneath and on legs.

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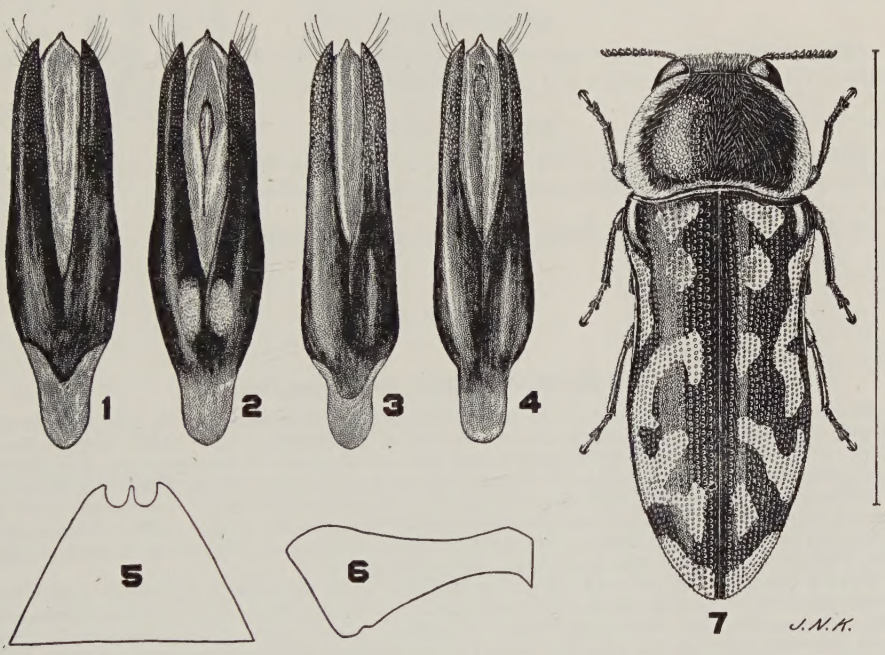
[1]Contribution from Department of Zoology and Entomology.

[2]The writer is indebted to Drs. R. H. Beamer and E. C. Van Dyke for the loan of material.

Head with front concave, surface irregularly, coarsely punctured; antennae not extending beyond middle of pronotum when laid along side, serrate from fourth segment.

Pronotum much wider than long, widest in middle, wider at base than at apex, side margins diverging to middle, then rounded, subparallel near base, margin carinate at base; anterior margin strongly sinuate; basal margin slightly sinuate; disk convex, with median depression and small transverse depression in front of scutellum; surface coarsely irregularly punctured, forming irregular smooth areas, punctures sparse on both sides of middle. Scutellum round, depressed in middle.

Elytra at base wider than widest part of pronotum; sides subparallel near base, expanded back of middle, then broadly rounded, sinuate near apices which are somewhat produced and



1. *Buprestis nuttalli* Kby., ♂ genitalia, dorsal view. 2. *Buprestis nuttalli* Kby., ♂ genitalia, ventral view. 3. *Buprestis consularis* Gory, ♂ genitalia, dorsal view. 4. *Buprestis consularis* Gory, ♂ genitalia, ventral view. 5. *Dicerca strandtmanni* n. sp., ♀ last ventral. 6. *Dicerca strandtmanni* n. sp., posterior coxal plate. 7. *Acmaeodera fisheri vermiculata* n. var., ♂, (line equals 5 mm.).

truncate, suture prolonged into a small spine; disk convex, a basal depression each side at umbone; surface coarsely irregularly punctured, with irregular depressed areas of dense punctures between smooth areas; punctures in rows along suture, suture carinate posteriorly from beyond middle.

Prosternal process flat, smooth, sparsely punctured. Hind coxae with posterior margin slightly sinuate internally, outer angle prolonged. Abdomen beneath coarsely, irregularly punctured, fifth ventral as illustrated, Figure 5.

Length 19.5 mm.; width 7.4 mm.

Holotype female in collection of writer labeled Texas, 1929, R. W. Strandtmann collector.

This species differs from other closely related members of the genus by truncate elytral apices, mucronate on inside, flat prosternal process and prolonged outer angle of posterior coxa.

It is possible that this may be a female of *D. mutica* Lec. Van Dyke[3] decided that *mutica* was a deformed specimen of *lurida* (Fab.).

[3]E. C. Van Dyke, Ent. News, 45, p. 91, 1935.

Buprestis prospera Csy.

This is a valid species. As pointed out by Casey[4] the intervals are more coarsely, confusedly, densely cribrate than *B. aurulenta* L. In addition the last visible ventral segment of abdomen is more broadly truncate in both sexes. Specimens are at hand from Arizona: Williams and south rim of Grand Canyon; New Mexico: Jemez Springs.

Buprestis consularis Gory

(Figs. 1, 2, 3 and 4)

An examination of the male genitalia convinces me that this species is distinct from *B. nuttalli* Kby. In addition to shape, the latter has a rugose area on ventral surface of genitalia near base.

Agrilus masculinus Horn

Adults reared from dead branches of Ohio buckeye (*Aesculus glabra* Wild.) collected in Delaware Co., Ohio, have vertex and pronotum brilliant cupreous, elytra black.

Agrilus champlaini Frost

This species makes galls on living blue beech (*Carpinus caroliniana* Walt.) in Crane Hollow, Hocking Co., Ohio. The swellings are similar to those formed on ironwood.

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[4]T. L. Casey, Proc. Wash. Acad. Sci., 9, No. 2, p. 122, 1909.

The Eye-Bank for Sight Restoration, Inc.

Extensive ophthalmic research which some day may enable many of the blind to see again, and will contribute greatly toward the prevention of blindness, is now under way in the laboratory of The Eye-Bank for Sight Restoration, Inc., at its national headquarters, 210 East 64th Street, it was disclosed here recently by Mrs. Aida de Acosta Breckinridge, Executive Director.

Although one of the principal objectives of the research carried on at the present time is the discovery of a method for the preservation of corneal tissue over a longer period of time than 72 hours, a variety of other problems in the field of ophthalmology are also being studied, according to Dr. Herbert M. Katzin, who is in charge of the laboratory.

During the past year, the Eye-Bank has granted seven fellowships for research and sixteen scholarships for its training course in the operation for the transplanting of healthy corneal tissue to blind persons who lost their sight because of corneal defects. Dr. Katzin has been developing special teaching methods to give surgeons the knowledge and skill required for this delicate operation.

Typical of the research projects carried on in the Eye-Bank's laboratory are studies to improve the surgical technique of corneal grafting and to perfect photographic methods for recording purposes; development of newly discovered properties of beta radiation in treatment of corneal scars; study of the use of physiological fibrin as a substitute for sutures, and development of methods for transplantation of the vitreous.

The technique of the corneal-graft operation which is taught and constantly perfected at the Eye-Bank has attracted such world-wide attention that it is beginning to serve as an institute for foreign ophthalmologists who wish to specialize in this field. Physicians from other countries who have come here and have had scholarships or fellowships from the Eye-Bank include:

Dr. John D. Blum, Geneva, Switzerland; Dr. Walter Kornbleuth, of the Hebrew University of Jerusalem; Dr. Geniniano de Ocampo, Manila, instructor in Eye, Ear, Nose and Throat at the Philippine General Hospital; Dr. M. K. Yue, Fukien, China; Dr. P. K. Kuo, Shanghai, China; Major M. M. A. Dubash, Bombay, India.

The operation substituting a healthy cornea for a damaged one can restore sight in only one type of blindness—that caused solely by opacity of the cornea when the rest of the eye and optic nerve are normal. It is estimated that 15,000 of the 250,000 blind persons in the United States can benefit from the corneal-graft operation.

More than a hundred leading hospitals throughout the country and many of the nation's outstanding eye surgeons are affiliated with the Eye-Bank. It is being greatly assisted by the co-operation of the Red Cross Motor Corps and important airlines in transporting eyes to the Eye-Bank and to hospitals.